Diatom communities in New Zealand subalpine mire pools: distribution, ecology and taxonomy of endemic and cosmopolitan taxa

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by

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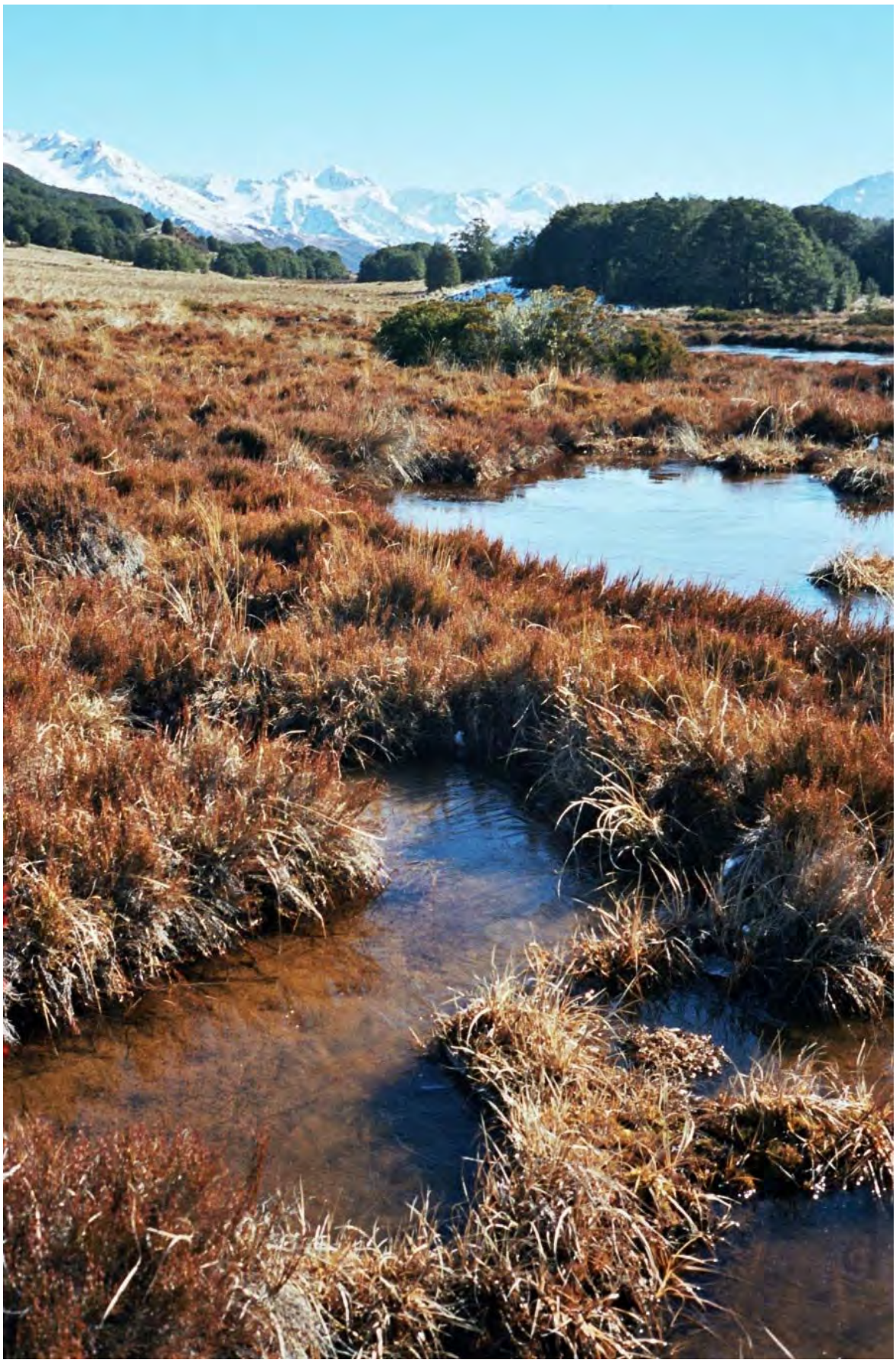
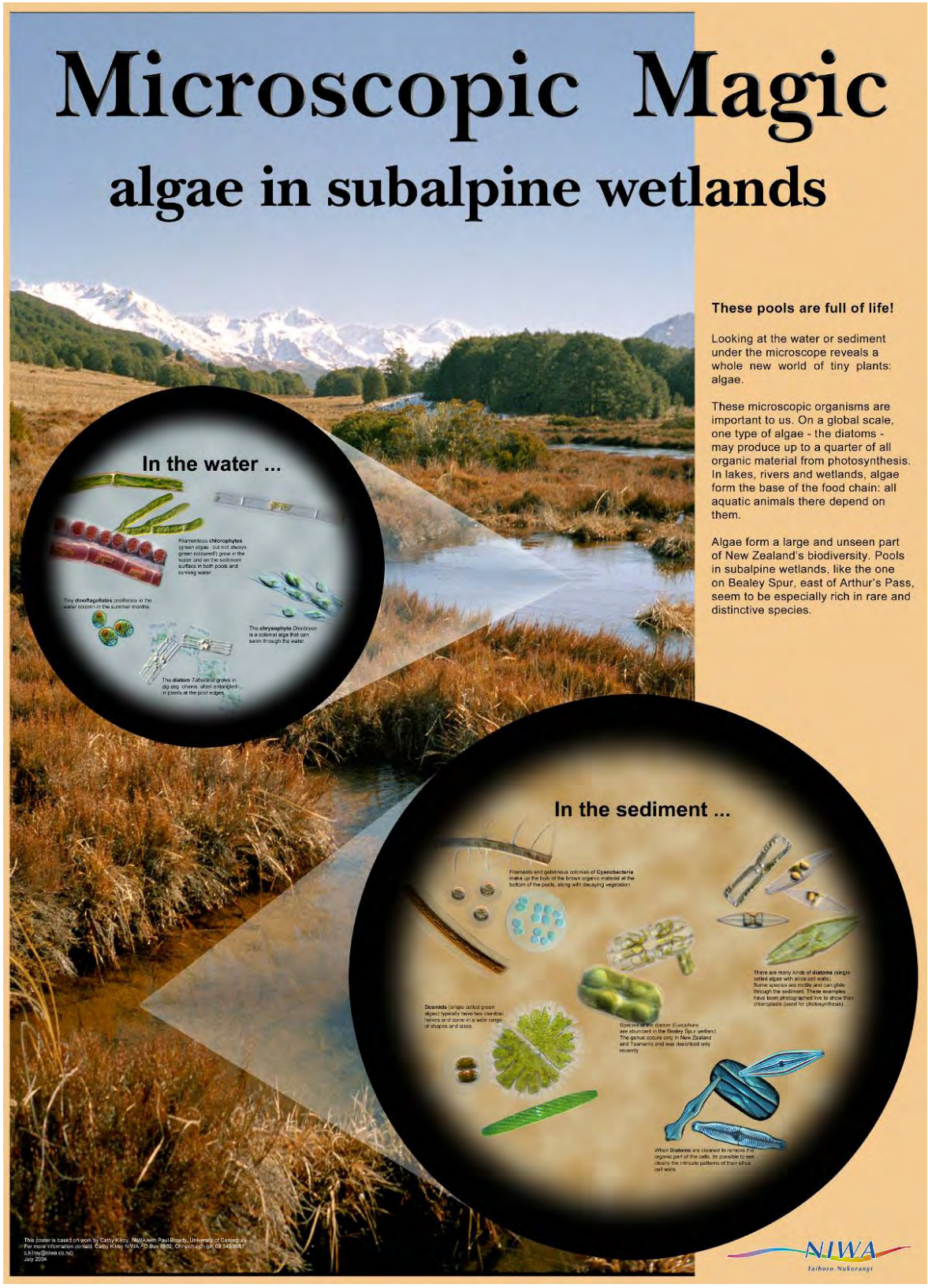


The mire pools at Bealey Spur, early winter



Poster showcasing the algal communities in the wetland (mire) at Bealey Spur, near Arthur's Pass, South Island, New Zealand.

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Abstract

Mire pools – shallow water-bodies in peat-forming wetlands – are a characteristic feature of New Zealand's subalpine and alpine landscapes (>1000 m a.s.l.), yet have been the subject of few biological studies to date, particularly of their algal communities. This research focuses on these subalpine systems, and on their diatom communities. Despite the established paradigm of ubiquitous dispersal in micro-organisms, recent taxonomic studies have confirmed a distinctive endemic component in the freshwater diatom flora of the New Zealand / Tasmania / East Australian region. In this study, I examined benthic diatom communities from >320 freshwater sites throughout New Zealand and showed that over 20% of species may be confined to this region. The endemic diatom species had highest densities in stable, unproductive environments, particularly in high-altitude mire pools and tarns. In most cases, non-endemic taxa coexisted with endemic species. This raised questions about (1) the special characteristics of mire pools and tarns (since endemism might be expected in areas that have unique environmental characteristics), and (2) the mechanisms that have allowed existing endemic taxa to withstand displacement by common cosmopolitan taxa, which, by definition, are successful colonisers. I addressed these questions using two years of data from four subalpine mire pools (Bealey Spur wetland, near Arthur's Pass, South Island). Physico-chemical data showed that water chemistry of these pools may differ from that of many Northern Hemisphere mire systems with respect to the relationship between pH and dissolved ions (especially calcium). This may be due to a combination of high pH rainfall, high rainfall quantities that limit the acidification effects of humic substances, and possibly vegetation differences. Therefore, some endemic taxa may be confined to these habitats because of the characteristic properties of the pools. I investigated the effects of disturbances in these stable environments. In the largest pool endemic species were shown to decline as wind-induced substrate disturbance increased. Endemic species also declined in two pools following small-scale experimental substrate disturbances. In all cases, non-endemic species remained unchanged. The distinctive species *Eunophora cf. oberonica* was responsible for much of the observed decline in endemic species abundances, which was evidently due to destruction of their specialised habitat within the cyanobacterial mats that made up the pool substrates. I explained pool-specific responses of diatom communities to disturbances by drawing on recent theory of invasibility as an intrinsic environmental property. I further investigated species coexistence by examining several general patterns of interspecific coexistence described for macroscopic organisms (e.g., abundance – occupancy, abundance – persistence). Patterns in mire-pool diatom communities were generally similar to those in larger organisms, and did not differ with respect to geographical range size (endemics vs. non-endemics), except at the scale of single pools. At this scale, endemic taxa, in particular *E.* cf. *oberonica*, can persist as dominant species. All the community analyses were underpinned by detailed taxonomic studies, from which I assessed over 40% of the more common

species in the pools to be either endemic or likely to be endemic. Two species occurring in the study area are formally described as new species. Overall, this work highlights the vulnerability of this hidden component of New Zealand's biodiversity to disturbances and environmental changes.

1. Introduction

Compared with macroscopic plants and animals, biodiversity of freshwater algae has received little attention globally (Norton 1996). At a regional level, freshwater algae are mentioned in New Zealand's Biodiversity Strategy as a group in which there are "sizable gaps in our knowledge" (Anon. 2000), despite the fact that algae provide much of the primary production in most freshwater systems (e.g., Stevenson 1996). This thesis addresses questions concerning one of the major types of algae in freshwater habitats: diatoms. Specifically, it addresses the distribution and maintenance of populations of endemic freshwater diatoms in New Zealand. Given current global concern about the homogenisation of biodiversity resulting from human-mediated biological invasions (Lovei 1997, Vitousek et al. 1997, Parmesan et al. 2005), recognition of a significant endemic component of this neglected group of organisms seems timely. Indeed, the issue has been highlighted by the recent accidental introduction into South Island rivers of the Northern Hemisphere freshwater diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt, with potentially serious consequences (Kilroy 2004, Kilroy et al. 2005).

The present study was initiated following observations on freshwater diatoms that appeared inconsistent with a well-known and controversial ecological paradigm concerning microbial distributions. In this introduction I first outline the paradigm and discuss its applicability to diatoms in general. Observations with respect to the New Zealand freshwater diatom flora are then described. A review follows of current knowledge about the habitats under study. The term "endemic", as used throughout the thesis, is defined and I explain my basis for distinguishing species and assigning endemic status to a species. I then introduce the questions to be addressed in the thesis along with a brief statement on the aims of the work.

1.1 Ubiquity in micro-organisms: applicability to freshwater diatoms

A common assumption in ecology is that species of micro-organisms are ubiquitous (Finlay and Clarke 1999, Fenchel and Finlay 2004). In other words, organisms less than about 1 mm long tend to have such large populations and disperse so readily that an eventual cosmopolitan distribution is inevitable, constrained only by the ecological tolerances of the particular organism (Finlay and Clarke 1999, Finlay 2002). First articulated by the Dutch microbiologist M.W. Beijerinck in 1913, the idea is encapsulated in the well-known axiom, "Everything is everywhere – the environment selects" (Baas-Becking 1934). The applicability of this paradigm has been debated from a number of perspectives and has generated lively controversy in the literature (e.g., Wilkinson 2001, Finlay et al. 2004, Mitchell and Meisterfeld 2005, Foissner 2006).

Recent meta-analyses have provided conflicting evidence. For example, a well-known "law" in ecology is the species–area relationship: species richness increases with the size of the area

sampled (Lawton 1999, Lange 2005). Explanations for the species–area relationship include: increasing habitat diversity as area increases; and colonization, speciation and extinction dynamics, i.e., as area increases, more species are encountered because physical / geographic barriers restrict species ranges, prevent colonisation and enhance speciation rates (Gaston and Spicer 2004). In other words, more endemic taxa contribute to diversity as the area sampled increases in size. A positive species–area relationship is a general pattern for larger organisms (see Gaston and Spicer 2004 for examples), but has been shown to be body-size dependent, with microbial organisms (e.g., diatoms) demonstrating the weakest relationships (Hillebrand et al. 2001, Azovsky 2002), implying a tendency towards broad or cosmopolitan distributions and less endemism.[1] On the other hand, Smith et al. (2005) found a strong species–area relationship for phytoplankton species, consistent with those reported for macro-organisms.

Another general "law" in ecology that has been argued to be related to body size is the latitudinal diversity gradient: a decline in species richness from the tropics to the poles (see review by Willig et al. 2003). Hillebrand and Azovsky (2001) found strong correlations for large organisms and virtually no relationships for microalgae. Again this was attributed to ease of dispersal by micro-organisms. A more recent analysis has revealed definite latitudinal diversity gradients in freshwater diatoms, suggesting that dispersal limitation may well be important (Vyverman et al. 2007)

As the latter two examples indicate, freshwater diatoms have been directly targeted in the ubiquity debate (see also Finlay et al. 2002). Diatoms (Ochrophyta: Bacillariophyceae) are single-celled, generally autotrophic, eukaryotic micro-organisms, usually included under the broad descriptor of "algae". The group is characterised by possession of a rigid silicified cell wall, which almost always conforms to a structure of two halves (each called a "valve"), and a series of silica hoops or bands (girdle bands), which extend the sides of each valve. These components fit together to form a three-dimensional structure (the "frustule"), which contains the cell organelles. The shape, size and patterning of the silica frustule form the basis for classification and identification of diatom taxa. Their distinctive and consistent structure means that diatoms are one of the best-defined algal groups. Excellent accounts of diatom structure, physiology, and reproduction exist in the literature (e.g., Round et al. 1990, Edlund and Stoermer 1997, Graham and Wilcox 2000, Chepurnov et al. 2004), therefore these topics are not elaborated upon here.

Diatoms are ubiquitous and extremely abundant in aquatic environments, occurring in both marine and freshwater ecosystems, and in all types of habitat which receive sunlight. In freshwaters, they inhabit both still and running waters across the entire spectrum of water types, from pristine oligotrophic lakes to eutrophic and polluted rivers and from damp rock walls to thermal springs (Round et al. 1990). In addition to being abundant, diatoms are also speciose.

[1] Note that the ubiquity theory does not completely rule out endemism in microbial species because of the existence of rare habitat types confined to certain geographical areas (Finlay et al. 2002).

Conservative estimates of the number of diatom species in existence are in the tens of thousands (Norton et al. 1996). Mann and Droop (1996) suggested that this should be revised to upwards of c. 200 000.

Finlay et al. (2002) argued that all freshwater diatom species have unlimited dispersal potential: if an environment is suitable for a species, then eventually that species will reach it. These authors maintained that: "The argument in favour of endemic diatom species is untenable, because it is not possible to disprove their existence elsewhere in the biosphere". Indeed there has long been wide acceptance that most freshwater diatom species have cosmopolitan distributions. However, Kociolek and Spaulding (2000) suggested that this view has been in part perpetuated by widespread use of northern European texts for identification purposes (e.g., Hustedt 1930, Krammer and Lange-Bertalot 1991-1997), and "matching" of local taxa to the descriptions for similar European species. Further, the mechanism for widespread dispersal of freshwater diatoms presents some difficulties. Benthic diatom taxa are not known to tolerate the desiccation that would necessarily accompany transport by wind (Mosich 2001, Gottleib et al. 2005, Kilroy et al. 2005), which has been frequently invoked as the major dispersal mechanism in diatoms (see discussion in Kociolek and Spaulding 2000). In addition, resistant spores that would facilitate wide dispersal have been recorded in only a very small number of freshwater benthic diatom taxa (McQuoid and Hobson 1996). In fact Kociolek and Spaulding (2000) suggested that truly cosmopolitan taxa occur mainly as a result of transportation by humans rather than natural dispersion, conceding that a core of 150-200 taxa may "occur across great ecological and geographical space that has been influenced by urbanization". A further argument against widespread natural ubiquity in diatoms is the rapidly accumulating body of data from regional studies. For example, Rumrich et al. (1998) documented many distinctive and presumably endemic taxa from the Andes; New Caledonia appears to be particularly rich in endemics (Moser et al. 1995, Moser and Lange-Bertalot 1998); many new species have been described from subantarctic islands (van der Vijver et al. 2002, Flower 2006) and new taxa continue to be described from the Northern Hemisphere (Lange-Bertalot and Metzeltin 1996, Siver and Hamilton 2005).

1.2 The New Zealand freshwater diatom flora

How does the New Zealand freshwater diatom flora conform to these opposing arguments? New Zealand was one of the last major land masses on Earth (apart from Antarctica) to be colonised by humans. Polynesians are thought to have arrived about 1000 years ago, and the first European settlers in the early 1800s. Geographical isolation and limited human influence should make New Zealand a good candidate area in which to demonstrate any regional distribution of diatoms. However, even the earliest collections were remarkable for comprising mostly cosmopolitan taxa. A few species from New Zealand were named by European diatomists in the 1850s, but the earliest known substantial collections of freshwater diatoms were made in Otago in the mid 1860s (Lindsay

1867). Unfortunately, the Gold Rush in progress at the time prevented Lindsay from carrying out his original plan of sampling over a wide area, extending to the Otago lakes and Southern Alps (Lindsay 1868). His collections were therefore confined to the Otago Peninsula and areas inland from Dunedin, and the main impression gained from them was of a predominance of "British forms". Subsequent collections were made in various parts of the country by amateur collectors, and the material was sent to European diatomists for analysis; again, with just a few exceptions, Northern Hemisphere forms predominated. Details of these historical collections and analyses of freshwater diatoms from New Zealand can be found in the interesting reviews by Dr Vivienne Cassie (Cassie 1983, Cassie-Cooper 1994).

The most comprehensive collections of New Zealand diatoms were undertaken in the 1970s in North Island (Foged 1979). Foged identified 525 species in 40 genera, of which he considered ~370 to be cosmopolitan, and: "Only very few (10-15 taxa apart from those described as new) are up to now shown only in Australia, Tasmania and New Zealand". However, Foged (1979) also commented: "The majority of the taxa is identical or almost identical with corresponding taxa known from other places in the world… Some others vary, however, rather much especially with regard to shape and size, but generally not more than seen elsewhere, and never so much that it should justify the establishing of a new species".

A similar reluctance by early diatomists to commit to new species was lamented by Mann (1999):

> 'Hagelstein (1939) noted that in Puerto Rico "endless differences in size, outline and striation, from published descriptions and figures have caused difficulty at times in making determination, and the author has frequently been tempted to propose new species". Unfortunately, he not only resisted this temptation but also chose not to document the "endless differences".'

A checklist of freshwater diatoms in New Zealand published over 20 years ago (Cassie 1984) listed approximately 800 taxa, and again highlighted the cosmopolitan nature of the flora.[2] Since then several focussed studies have suggested that, in parallel with the increasing evidence for freshwater diatom endemism globally, there are likely be many more regionally distinctive taxa in New Zealand than previously suspected. Three examples follow.

1. A critical examination of New Zealand populations of *Gomphoneis herculeana* (Ehrenberg) Cleve showed clear discrimination on the basis of shape from other *G. herculeana* populations (Stoermer et al. 1986). The New Zealand taxon was subsequently transferred to a new, presumed endemic, variety *G. minuta* var. *cassieae* Kociolek and Stoermer (Kociolek and Stoermer 1988).

[2] A more recent checklist (in Harper et al. in press) contains just 11 new records, but is an unannotated species list only, not including references to the source of records as the earlier checklist does.

2. Preliminary collections of material from high-altitude tarns in the South Island in the early 1990s yielded a few specimens in the genus *Eunophora*, recently discovered in similar habitats in Tasmania (Vyverman et al. 1998). Subsequent collections showed that not only was the genus widespread (from South Island and Stewart Island), but that at least two species were common (Vanhoutte et al. 2006b). The New Zealand distribution was documented in the formal description of the genus (Vyverman et al. 1998). Interestingly, one species was already known in New Zealand – as *Amphora berggrenii* Cleve – described from fossil material at Arthur's Pass (Cleve 1881). *Eunophora* is a distinctive genus with close affinities to *Eunotia*. To date no similar taxon has been reported from anywhere else, despite international requests for records (K. Sabbe, University of Gent, pers. comm.).
3. Three new species of the predominantly Southern Hemisphere genus *Actinella* (*A. aotearoaia* Lowe, Biggs and Francoeur, *A. indistincta* Vyverman and Bergey and *A. pulchella* Sabbe and Hodgson) were described from New Zealand material as part of a suite of species newly recognised from Australia, New Zealand and Papua New Guinea. *A. aotearoaia* has thus far been found in New Zealand, where it can be locally common, and eastern Australia (Sydney). Both *A. indistincta* and *A. pulchella* are known from New Zealand (Stewart Island) and Tasmania (Sabbe et al. 2001). Both species were found in slightly acidic flowing waters, habitats that had hitherto received little attention from diatomists.

Current understanding is that endemism in freshwater diatoms in New Zealand is still unusual. Harper et al. (in press) estimated 2.3% endemic freshwater diatom taxa, based mainly on Foged (1979). However Vyverman et al. (1998) and Sabbe et al. (2001) present evidence of a much more regionally distinctive freshwater diatom flora, in particular centred on relatively unexplored habitats. Additionally, *Eunophora* spp. and *Actinella* spp. were not the only unusual diatom taxa present in samples from these habitats (personal observations). Further, the analysis by Stoermer and Kociolek (1986) suggests that more detailed scrutiny may show that other common freshwater diatom taxa are in fact regional variants. Interestingly, one common diatom species encountered frequently by Foged (1979) was already recognised as a Southern Hemisphere species. *Cymbella kappii* Cholnoky resembles *Cymbella affinis* Kützing (cosmopolitan, according to Krammer and Lange-Bertalot 1991-1997), in shape, size and striation, but differs in the number and location of central stigmata (isolated puncta at the centre of the cell). *C. kappii* had been previously recorded in South Africa, Sri Lanka and Eastern Australia, but not in the Northern Hemisphere, where, to my knowledge it has still not been reported. Hence some degree of regionalisation in diatom distributions has long been evident. At the same time, there is no escaping the fact that a remarkable proportion of New Zealand's freshwater diatom flora is morphologically indistinguishable from that of the Northern Hemisphere.

1.3 Diatoms in tarns / mire pools and related habitats

Many of the recently described regional diatom species in New Zealand have been found in small alpine or subalpine water bodies. In the South Island, these generally formed during glacial retreat at the end of the last ice age (for general descriptions of the origins of various types of wetlands and small water bodies, see Johnson and Gerbeaux 2004) and include tarns (small, isolated lakes in glacier-formed depressions) and mire pools (shallow open waters in wetland areas raised on a base of accumulated organic material (Gore 1983)). A review of research on lakes in New Zealand (Burns 1991) indicated that up until that time, benthic algal communities had received little, if any, attention in either large or small lakes. Since that review, there has been limited research focussing on lake benthic algae (e.g., Hawes and Smith 1993, 1994), and several studies including reference to epilithic and epiphytic algal communities (e.g., Miller and Death 1997; James et al. 2000). However, most recent research has been in relation to medium to large-sized lakes (see references in Vanhoutte et al. 2006a). The only study specifically on diatoms was a first attempt to construct a transfer function using diatoms for the prediction of lake water chemistry (nutrients, pH) (Reid 2005), again in medium to large-sized lakes only. Overall, in New Zealand there is very little published information about algal communities in small alpine or subalpine lakes, or indeed, in mires and wetlands in general, though there are exceptions. Skuja (1976) documented 105 diatom species in bog / wetland habitats around New Zealand, all of which were assigned to cosmopolitan taxa, but only one of which was illustrated. Burns et al. (1984) recorded 18 diatom genera in "morainic ponds" near Lakes Tekapo and Ohau, but their main focus was the invertebrate fauna. The only other significant work on algae in tarns appears to have been taxonomic studies on the desmid flora (e.g., Flint 1996; Flint and Williamson 1999).

Other research has concentrated mainly on vegetation and vegetation history of wetlands associated with tarns (e.g., Burrows 1972, Campbell 1983, Merton 1987, Mark et al. 1995), and water chemistry (Dickinson et al. 2002). Palaeoecological investigations in wetlands and tarns in New Zealand have employed a number of markers (pollen and macrofossils, Moar 1977; pollen, McGlone et al. 1995), but none, to date, has used diatoms. There are several unpublished reports on the vegetation and ecology of tarn and wetland areas in South Island, including, for example, Wardle (1981,Tutaki Valley, Nelson); Johnson (1980, Lake Ohau tarns); Johnson (1984, Tarndale). These, and others (e.g., Campbell 1983), have emphasised the need for conservation of these environments because of their unique vegetation assemblages. Again, none considered the algal communities. Indeed, the fact that live *Eunophora* has only been "discovered" in New Zealand in the past 10 years is a reflection of the lack of studies on diatom communities in alpine / subalpine water bodies. Given that there are at least 7500 mappable waterbodies < 1 ha in area and located more than 600 m a.s.l. throughout New Zealand (NIWA data, Helen Roulston, pers. comm.), such a paucity of information is surprising.

Internationally, numerous studies of diatoms in small lakes, tarns and wetlands have been conducted as part of palaeolimnological investigations and the construction of calibration sets for the evaluation of past and future environmental changes (e.g., Gasse 1978; Bennion 1995; Douglas and Smol 1995; Vyverman et al. 1996, Michelutti et al. 2003). Mire and wetland pools have also been targeted in a number of taxonomic and ecological treatments of algae, including diatoms (Scherer, 1988; Mataloni and Tell 1996; McCormick et al. 1996; Mataloni 1999; Watanabe et al. 2000; Owen et al. 2004, Gottlieb et al. 2005). As a result the diatom flora of these environments in other parts of the world is reasonably well documented.

1.4 A New Zealand–Tasmania–Eastern Australia biogeographic region?

The definition of endemic is: “regularly or only found among (specified) people or in (specified) country” (Concise Oxford Dictionary, seventh edition 1982). The implication is that the geographical range must be defined. As indicated in the above discussion, it appears that some of the distinctive diatom species identified from New Zealand in both recent and past taxonomic studies also occur in Tasmania and Eastern Australia (Foged 1979, Vyverman et al. 1998, Sabbe et al. 2001). This could be interpreted as evidence that no endemism exists in diatoms in New Zealand. However, explanations for the origins of vascular plants in New Zealand can readily be reconciled with a New Zealand–Tasmania–Eastern Australia bioregion for diatoms.

Although a small component of the New Zealand vascular plant flora may be explained by vicariance (i.e., derived from the remnants of Gondwanan flora), current evidence points strongly to dispersal as the main origin of the current flora (McGlone 2005, Trewick et al. 2007). McGlone et al. (2001) examined patterns of endemic and non-endemic plant distributions in New Zealand and found clear correlations between the occurrence of endemism and both ecological factors and dispersal abilities (or lack of them), both of which indicated a significant role for dispersal as opposed to vicariance. The proposed explanation was that from the late Oligocene (ca. 25 M years ago) to late Miocene (ca. 10 M years ago), when the climates of the Eastern Australian and New Zealand regions were similar, prolific dispersal occurred from Australia, especially of woody plants. Subsequent climate differentiation and mountain formation in New Zealand slowed the rate of immigration of taxa except for the more dispersible groups. Radiation of species within New Zealand since that time has resulted in the many endemic plant taxa seen today.

Major speciation of freshwater diatoms into recognisable “modern” taxa pre-dated this major plant-dispersal period (Sims et al. 2006). Therefore it is conceivable that similarities in the diatom floras of New Zealand and Australia originated at the same time as the plant dispersal. Thus a biogeographical region encompassing New Zealand, Tasmania and Eastern Australia appears

logical for diatoms, particularly as speciation rates in raphid diatoms[3] can be slow (Kooistra and Medlin 1996). More recent dispersal events across the relatively short distance of the Tasman Sea are of course possible, as has occurred in some plant groups (ferns, wetland plants; McGlone et al. 2001).

1.5 Defining diatom species

Characteristic patterning of the silica cell walls of diatoms, along with cell shape and size have traditionally been used as the basis for distinguishing species. Following the discovery of diatoms in the 18th Century[4], the apparent ease with which taxa could be identified – given a good microscope – made them a fashionable topic for study. Diatomists of the 19th Century such as Ehrenberg, Kützing and Greville named and illustrated numerous species from all over the world, many of which are still considered valid today. Nevertheless, in a comprehensive critique of the concepts and philosophies adopted by these and other early diatom taxonomists in their allocations of specimens to genera, species and varieties, Mann (1999) concluded that: "… in many cases, diatomists might just as well have been classifying scraps of wallpapers as diatoms". Mann's main points were: (1) the traditional approach to classification of diatoms based principally on analysis of the silica frustule severely underestimated the true number of diatom species in existence, if a biological species concept were to be applied;[5] and (2) such an approach could lead to serious misrepresentation of the relationships among taxa. A further theme in Mann's review was that early taxonomists often assumed cosmopolitanism in diatom species on the basis of similarity of shape, whereas closer examination of both morphological *and* developmental features was expected to reveal not only many more species, but also much more geographical differentiation of species (Mann 1999; see also Mann and Droop 1996).

Mann's view has been strongly reiterated in a recent review of the evolution of diatoms (Sims et al. 2006), which raises a potential problem for the present study. Sims et al. (2006) maintain that: "Species-level classification in diatoms is … a poor and uneven foundation for studies in ecology

[3] Raphid diatoms are generally pennate (elongated) taxa (though there are round-shaped species), distinguished from centric (radially symmetric) and araphid taxa by the possession of a pair of longitudinal slits in one or both valves, together termed the raphe. Pennate raphid diatoms evolved later than centrics and araphid pennates, but this structure allowed diatoms to invade many new benthic habitats since it facilitates motility. Most of the endemic taxa referred to in this study are biraphid pennates (having a raphe on both valves).

[4] The first recorded occurrence of a diatom was in 1703, when an anonymous contributor described what was almost certainly the freshwater diatom, *Tabellaria flocculosa*, in a paper communicated to the Royal Society of London (Round et al. 1990).

[5] Paradoxically, some early diatom taxonomists did observe and illustrate the cellular features of diatoms, and distinguished genera on the basis of chloroplast type in addition to shape and frustule ornamentation. In some cases, subsequent re-classification combined these taxa with other species on the basis of the frustule features alone. Only recently have these genera been re-assigned to their original nomenclature. Examples are the genera *Sellaphora* (Mann 1989) and *Placoneis* Merechowsky (Cox 1987).

or biogeography, or even phylogeny…" and "The semicryptic and cryptic species that are beginning to emerge cannot be assumed to have similar ecologies….". Extended to its logical conclusion, this view implies that species cannot be reliably identified on the basis of morphology alone. Indeed, the sympatric existence of sexually separated yet morphologically *similar* species of diatoms has been demonstrated (Mann et al. 2004), though in this case subtle – but consistent – morphological differences also separated the species. Identification of cryptic species from genetic differences is potentially a more difficult problem because morphologies may be *identical*. However, the significance of such genetic differences in eukaryotic aquatic microbes is by no means universally accepted (Dolan 2005, Fenchel 2005, Lowe et al. 2005), and there have been recent pleas for a greater effort to describe culture-resistant microbial species by phenotypic rather than genotypic characteristics (Fenchel and Finlay 2006).

A review of recent studies comparing morphology, molecular structure and occasionally reproductive patterns in diatoms shows that in general the genetic and morphological structures of diatoms correspond very well, though there are exceptions. For example, *Pseudo-nitzschia delicatissima* has been distinguished from *P-n. decipiens* and *P-n. dolorosa* on the basis of subtle, but consistent morphological differences, and clear molecular differences. At the same time, large variation was found in the ITS (internal transcribed spacer) region of the *P-n delicatissima* genome, with no detectable morphological discrimination (Lundholm et al. 2006). Cryptic diversity in this species was also found by Orsini et al. (2004), although minor morphological differences were also noted. *Cyclotella scaldensis* has been separated from *C. meneghiniana* on the basis of morphological and molecular differences, but further morphologically undifferentiated strains of *C. meneghiniana* have been identified (Beszteri 2005). Two genetically different forms of *Navicula phyllepta* can also be separated morphologically and ecologically (Créach 2006). Species originally grouped under *Skeletonema costatum* have been separated into at least four additional species on both morphological and molecular grounds (Sarno et al. 2005). Further species of *S. costatum* have been distinguished by Chen et al. (2007).

Observations on mating are now being added to the suite of techniques used to establish relationships among species. The classic studies on *Sellaphora* (Mann et al. 2004) have confirmed that morphologically close species previously lumped together into the same taxon can coexist in the same environment and remain reproductively isolated from each other. At the same time, morphologically identical forms of *Sellaphora* from populations thousands of kilometres apart are also genetically identical and capable of interbreeding (Behnke et al. 2004). Similarly, *Eunotia bilunaris* from Tasmania and New Zealand have also been shown to mate successfully (Vanormelingen et al. 2007).

These examples illustrate a number of points:

(1) existing diatom species previously presumed to have wide cosmopolitan distributions may actually comprise a whole suite of separate species which can be clearly separated using molecular techniques;
(2) in many cases (though – importantly – not all), the separate species can also be distinguished morphologically;
(3) these morphological differences are often subtle, and sometimes not obvious until the fine structure is examined using scanning electron microscopy;
(4) nevertheless the fact that morphological differences can very often be discerned suggests that morphology remains a useful means of distinguishing species, *as long as detailed comparisons are made with related species, using good quality illustrations or original material, and the species of interest are themselves well documented (including archiving of reference material) to aid future comparisons.*

Consequently, despite the controversy, it is possible to justify identification of species – and their separation into endemic and non-endemic groups on the basis of frustule morphology. In addition to the qualifications mentioned in (4) above, it is also essential to examine populations of each species, rather than individuals. This enables definition of the size range (with associated shape changes) of each species. It should be acknowledged that some species assigned cosmopolitan status may in fact belong to clades of genetically differentiated taxa that are morphologically similar or identical. However, species classed as endemics should be morphologically distinct from any species described from the Northern Hemisphere. While possible cryptic species may also be endemic, morphologically distinctive taxa appear far more likely to have been long-separated geographically from related taxa in other regions.

1.6 Research questions

As suggested in the foregoing discussion, the presence of more apparently endemic freshwater diatom taxa in New Zealand than previously suspected (using the definition in section 1.4) raised doubts about the general applicability of the ubiquity theory to diatoms.
If endemic diatoms conform to general theory developed with reference to macro-organisms (principally terrestrial plants), this would lend support to the proposal that geographical range sizes of diatoms can be constrained by dispersal, and that the ubiquity assumption is not universal in this group. Comparisons between macro- and micro-organisms (including diatoms) with regard to diversity patterns have been undertaken (Hillebrand and Azovsky 2001, Hillebrand et al. 2001), but as far as I can ascertain, no previous studies have examined the distributions of microorganisms on the basis of their geographical range sizes in relation to regional habitat characteristics.

Therefore my first question was:

Is there any pattern to the occurrence of endemic freshwater diatom taxa in New Zealand, in terms of the habitats in which they are found, and can this be reconciled with existing ecological theory?

Subsequent research questions stem directly from the results of the above analysis, in which I found that tarn / mire pool habitats, on average, support diatom communities comprising higher proportions of endemic diatoms (estimated as total biovolume across all species) than other habitat types. Thus, the second research question is:

What characteristics of tarn/mire pool environments allow them to support high proportions of endemic and unusual taxa?

There are at least two ways to approach this question. First, we could examine the environmental characteristics of tarns / mire pools and look for relationships with abundances of different diatom taxa, both endemic and non-endemic. Second, we could compare these environments in New Zealand with similar environments overseas to determine whether there is anything unusual about them. Unique environments that also conform to the general conditions favouring endemism would be expected to accumulate endemic species, regardless of the dispersal abilities of the organism group as a whole.

From the perspective of diatom species that might potentially colonise these habitats, a third question can be formulated:

What are the characteristics of tarns/mire pools that might select against competing cosmopolitan taxa and allow coexistence with endemic taxa?

Again, this question can be tackled from various perspectives. Assuming that the initial multi-habitat analysis (the first question) will indicate general features that favour endemism, it should be possible to formulate testable hypotheses to confirm the effect of these features at a local scale. Another approach would be to look at the community patterns at a range of scales, and in the context of traditional and contemporary theories for explaining species coexistence.

In summary, the primary objectives of the research are to identify any patterns of endemism in diatoms in New Zealand, and then to investigate the maintenance of these patterns in a representative area where endemic diatom taxa (particularly the distinctive endemic genus *Eunophora*) are abundant. The monitoring and experimental components of the study are underpinned by taxonomic studies. The latter comprised examination and photographic documentation of diatom taxa in the study area, and comparisons with published descriptions and illustrations of similar taxa, to establish the distribution status of each species (non-endemic or endemic).

It is hoped that the work described in this thesis will improve understanding of the following:

1. Patterns of microbial biodiversity and distinctiveness in New Zealand by identifying habitats likely to support communities of endemic/regional diatom species, which may also be indicative of pristine environments;
2. The physical, chemical and biological environment in shallow subalpine bog pools and tarns, which have hitherto been relatively unstudied, despite being characteristic and attractive features of the New Zealand alpine and subalpine landscapes;
3. Global biodiversity patterns in freshwater diatoms (specifically, taxa with restricted geographical ranges) and the potential effects of habitat modification and global climate change on the survival of these species.

The first two aims are expected to provide information to guide any future management of tarns / mire pools in New Zealand. Although most are already protected within New Zealand's Conservation Estate, a better appreciation of their special values, and the possible effects on these of both climate and direct anthropogenic changes, may assist in future decision-making relating to areas containing these features.

1.7 Thesis structure

The work undertaken for this thesis has been written up as seven papers. Following this introduction to the research (Part 1), the individual papers are presented in Part 2, as Sections I to VII. The seven papers are listed below, along with notes on their relevance to the research questions, and a statement about any parts of the work where I obtained assistance from others. At the time of submission of this thesis, three of the papers have been published, and one has been accepted for publication subject to minor revision. The remaining three are under peer review. I provide a synthesis of the work, with conclusions, in Part 3. All references are collated into a single list in Part 4. Throughout Parts 2 and 3, the seven papers (below) are referred to by their roman numeral, along with the published reference, where appropriate.

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I. Kilroy, C., Biggs, B.J.F., Vyverman, W. (2007). Rules for macroorganisms applied to microorganisms: patterns of endemism in benthic freshwater diatoms. Oikos 116: 550-564.

This paper describes a landscape-scale analysis of diatom communities from >320 sites in New Zealand, spanning the whole range of freshwater habitats. The analysis addresses the first research question of the thesis (Section 1.6) by assigning species found in each community to distribution categories ranging from endemic to cosmopolitan. Indices of disturbance and productivity were derived for each site, and proportions of endemic taxa within the disturbance vs. productivity matrix were compared with a model predicting endemism. The basis of the analysis was an existing collection of diatom samples collected from 1997 to 2004 as part of a New Zealand Foundation of Research, Science and Technology-funded Freshwater Biodiversity programme. The samples were

collected by a range of people (including myself) using standard methods (including documentation of environmental/habitat information), which I supplied. I received assistance from NIWA colleagues in slide preparation and microscope photography, under a grant from the Department of Conservation in their Terrestrial and Freshwater Biodiversity Information Systems scheme (TFBIS project no. 69). I undertook the balance of the work, including all species identifications, data analyses, and manuscript writing/preparation.

II. Kilroy, C., Biggs, B.J.F., Vyverman, W., Broady, P.A. (2006). Benthic diatom communities in subalpine pools in New Zealand: relationships to environmental variables. Hydrobiologia 561: 95–110.

This is an account of a synoptic survey of 20 sites in my primary study area, a wetland / tarn / mire pool complex on Bealey Spur, near Arthur's Pass, Canterbury. In this paper I first confirmed the findings in paper I, that bogs and tarns are most likely to yield high proportions of endemic diatom taxa. My aim was then to look for species – environment relationships, and in particular to identify any patterns associated with the most common endemic diatom taxa present, two species of *Eunophora*. Both aims are relevant to the research question (p. 13): What characteristics of tarn/mire pool environments allow them to support high proportions of endemic and unusual taxa? This paper also provides a description of the study area which is referred to in subsequent papers. I undertook all sample collection, diatom processing and analyses, data analyses and manuscript writing / preparation in this project. Most of the water chemistry analyses were undertaken in commercial laboratories.

III. Kilroy, C., Biggs, B.J.F., Vyverman, W., Broady, P.A. (accepted subject to approval of revision). Spatial and temporal variability in mire pool limnology. Fundamental and Applied Limnology

Environmental conditions in the study area were summarised in paper II based on a single sampling occasion. In this third paper, I analysed two years of data I collected on the physico-chemical variables at four sites in the study area in order to (a) quantify physico-chemical habitat variability over space and time, and (b) assess overall chemical gradients at these sites and compare them with published data from other parts of New Zealand and from the Northern Hemisphere. This paper again addresses research question 2, including identification of apparently unusual conditions in the study area, where endemic diatom species occurred in very high proportions. I carried out all sample collection (with occasional assistance), some laboratory analyses, and all data analyses and manuscript writing / preparation in this project. Data from Tasmanian mire pools was contributed by the third author. Most of the water chemistry analyses were undertaken in commercial laboratories.

IV. Kilroy, C.; Biggs, B.J.F. (under peer review). Disturbances and invasibility control endemism levels in a freshwater diatom community.

The results of the New Zealand-wide analysis in paper I indicated that highest endemism in freshwater diatoms was to be expected in low disturbance habitats, particularly where resource supplies (nutrients) were also low. This to some extent suggests an answer to research question 3 in the form of a testable hypothesis, viz., a lack of disturbances and low nutrient supplies in these environments, combined with low intrinsic invisibility, allows for the stable coexistence of endemic taxa and only those cosmopolitan taxa that have already succeeded in colonising the sites. In this paper I describe field observations and experiments in which this hypothesis was tested. I carried out all sample collection (with occasional assistance), all sample and data analyses, and all manuscript writing / preparation in this project.

V. Kilroy, C., Biggs, B.J.F., Vyverman, W., Broady, P.A. (under peer review). Coexistence of endemic and non-endemic benthic diatoms: the roles of scale, community dynamics, and environmental interactions.

In this paper I explain the coexistence of endemic and cosmopolitan taxa (research question 3) at different scales using data from mire pools throughout the South Island (a subset of the data used in paper I), from multiple pools in a single mire system (from paper II) and a two-year dataset of diatom taxa abundance at four sites in the study area at Bealey. I carried out all sample collection (with occasional assistance), all sample and data analyses, and all manuscript writing / preparation in this project.

VI. Kilroy, C. (under peer review). Taxonomy of benthic diatoms from subalpine mire pools.

This manuscript comprises detailed descriptions of twenty-eight diatom taxa found at the study area along with comparisons with similar taxa and justification for classification as either endemic or cosmopolitan. This work underpins the conclusions in papers IV and V. Note that much of the work was undertaken in order to establish species identities in papers I and II. I have obtained additional references (including newly published material) since paper II was completed, and this has lead to a few changes in species assignments. This has not altered the overall conclusions about the distributions of species. The work has resulted in provisional assignment of “previously undescribed” status for 12 species, all of which I consider to be likely endemics. At least one of these may extend in its range to Tasmania. Formal species descriptions are planned (currently beyond the scope of this thesis), in collaboration with diatomists familiar with the Tasmanian and Australia flora. I undertook all sample collections, processing, photography, species comparisons, and manuscript writing / preparation.

VII. Kilroy, C.; Sabbe, K.; Bergey, E. A.; Lowe, R.L.; Vyverman, W. (2003). New species of *Fragilariforma* (Bacillariophyceae) from New Zealand and Australia. New Zealand Journal of Botany 41: 535–554.

This paper is a formal taxonomic description of two new species of the diatom genus *Fragilariforma*, which are further examples of recently discovered distinctive freshwater diatom taxa which are endemic to the New Zealand–Tasmania region. Both species were present in low densities at some sites in the main study area used in this thesis, though the type localities were pool / bog habitats on, respectively, Jordan Saddle (Arthur's Pass, approximately 2 km from the study area), and Stewart Island. The results of this work contributed to assignment of species distributions in papers I and II, and further demonstrate the detail necessary to establish the identity of a new species. The Tasmanian component of the description (including some photographs) was contributed by the second author, along with part of the discussion. Sample collection of the New Zealand material was undertaken with the third author, who also took some of the SEM photographs. I carried out all other species comparisons, photography and manuscript writing and preparation.

2. Original papers

2.I Rules for macro-organisms applied to micro-organisms: patterns of endemism in benthic freshwater diatoms

Introduction

Debate about global and regional patterns in species range sizes has long featured in the ecological literature, with most attempts to identify patterns or test hypotheses focusing on macroscopic organisms (Gaston 2003). Superimposed on this debate has been discussion about different "rules" operating for microscopic organisms (Dolan 2005). In particular it has been suggested that microorganisms <1 mm in length are so abundant and so easily dispersed that an eventual cosmopolitan distribution is inevitable, and only environmental tolerances limit the geographical distribution of each species (Finlay 2002, Fenchel and Finlay 2004). In contrast, reviews focussing on diatoms have argued that range size in these organisms can be constrained by dispersal potential (Mann and Droop 1996; Kociolek and Spaulding 2000). However, the question of whether microorganisms believed to be endemic conform to patterns observed in larger organisms has not been investigated. Consistency between observed patterns of endemic macroscopic organisms and those of suspected endemic diatoms would lend support to the proposal that range-size limitation has a role in structuring diatom communities.

Huston (1994) discussed endemism in the context of the dynamic equilibrium model (DEM), which predicts species diversity from the interaction between rates of competitive exclusion (determined by productivity) and rates of disturbance. Using mainly terrestrial plants as examples, he proposed that the low rates of competitive displacement in low-productivity environments allow the accumulation of endemic species because there are fewer resources to invest in reproduction and effective dispersal mechanisms (such as inducements for dispersal by birds). Further, although stable, low productivity environments are considered susceptible to invasions, *dominance* by new colonizers is unlikely (Huston 2004). As a result such environments would be expected to contain the highest proportions of native taxa (including endemics) unless there is a major change to the disturbance regime or an increase in resource availability (Davis et al. 2000).

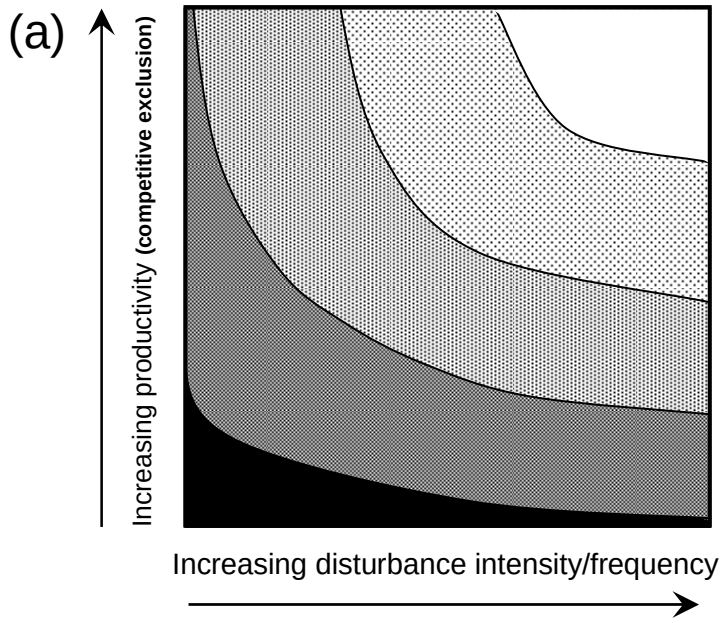
The ideas encompassed in the DEM in relation to endemism are consistent with the concept of invasibility as an intrinsic, dynamic property of biological communities, driven by disturbance regime, resources and prior colonisation from a regional species pool (Davis et al. 2005). Many studies have shown that maintenance of native diversity is not necessarily directly threatened by new colonists (Lonsdale 1999, Stohlgren et al. 1999, Gilbert and Lechowicz 2005). However disturbance in a stable environment may increase invasibility and result in dominance of colonists (invaders) at the expense of local species, particularly where resources are high (Burke and Grime

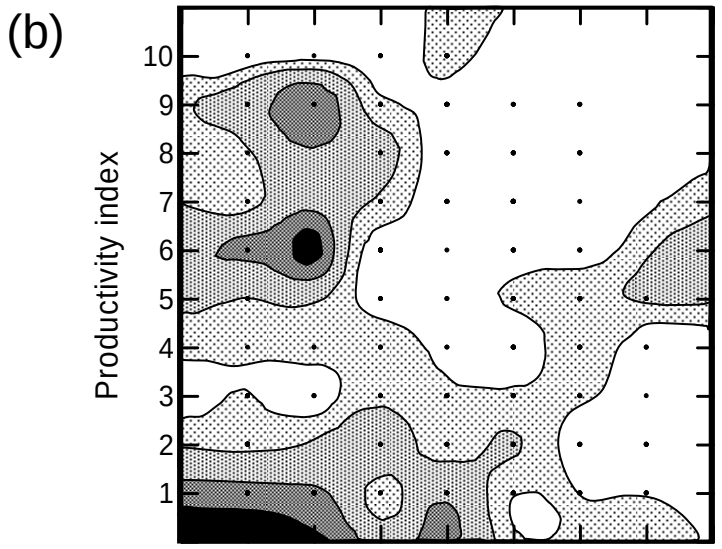
1996). On the other hand, in unproductive environments, low invasibility may be associated with high disturbance levels through low potential for colonization potential by any species (Huston 2004).

An explicit model for the environmental conditions that favour endemism can be inferred from the above, and results from: the maintenance of endemics in low productivity environments including those experiencing some disturbance; the low probability of dominance by exotics (invaders) in stable, low-productivity environments; and high probability of dominance by invaders in productive, disturbed habitats (Figure I.1a). An important component of the DEM argument is that geographic isolation is not a necessity for maintaining endemic populations or even for generating them (Huston 2004).

Given both old and new exceptions to the paradigm of universal cosmopolitanism in diatoms (Foged 1979, Vyverman et al. 1998, Sabbe et al. 2001, Kilroy et al. 2003), these organisms provide a suitable system for investigating the DEM explanation for maintenance of restricted range sizes. In combination with the concept of invasibility (Davis et al. 2005) the model may also explain the ability of diatom species with restricted range sizes to maintain thriving populations alongside cosmopolitan taxa. The DEM for species richness has been shown to explain patterns of species diversity more completely than alternative theories in a number of recent studies, for example, for marine phytoplankton (Agard et al. 1996); wetland plants (Pollock et al. 1999) alpine plant communities (Kammer and Mohl 2002); stream benthic algae (Biggs and Smith 2002). As far as we are aware, there has been no previous attempt to examine patterns of endemism in the context of the model.

In this study, we used data on diatom community composition, with associated habitat information, to explore landscape-scale patterns of freshwater diatom communities in New Zealand in terms of the range size of species (endemic vs. Southern Hemisphere and cosmopolitan). We defined an endemic diatom taxon as one with a maximum known range covering the New Zealand – Tasmania – Eastern Australia region, in other words Australasian endemics. This biogeographical region can be explained by considering the New Zealand vascular plant flora, which largely originated through dispersal from Australia via westerly wind drift, with subsequent development of different species as environments in the environments in the two areas differentiated (McGlone et al. 2001, Cook and Crisp 2005). Thus, it is not surprising that many of the distinctive diatom taxa in New Zealand are shared by the Tasmanian /Eastern Australian flora in areas which have retained environments similar to that of New Zealand. Our aims were: (1) to determine the occurrence of endemic and cosmopolitan diatom taxa across the entire range of freshwater environments; (2) simultaneously, to empirically test the applicability of the DEM for explaining distributions of endemic diatom species within New Zealand. We briefly consider mechanisms that may explain the co-existence of endemic and cosmopolitan diatom taxa, assuming that some fast-growing and





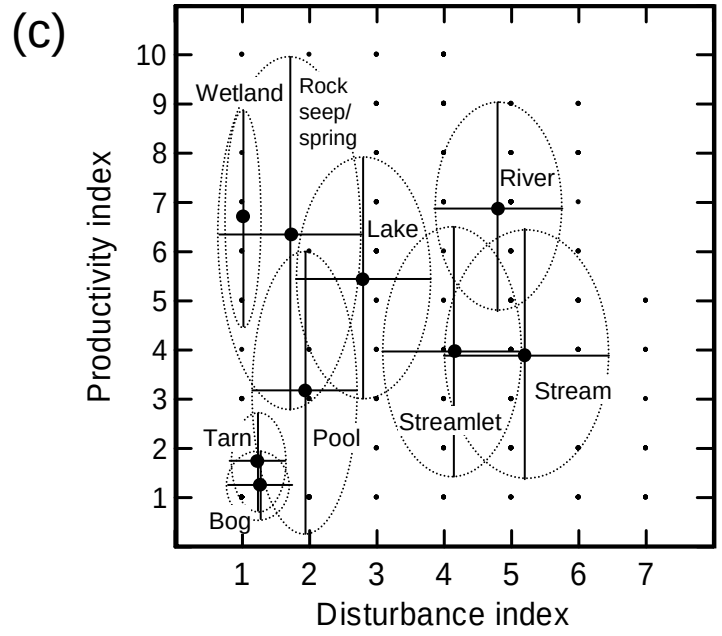


Figure I.1.

(a) Expected relative occurrence of endemic taxa in habitats described in terms of disturbance and productivity, adapted from the predictions of the Dynamic Equilibrium Model with axes reversed (Huston 1994). Darker shading represents higher probability of occurrence of endemic taxa. The maintenance of endemic taxa is favoured by low rates of competitive exclusion (low-productivity environments) and low rates of disturbance.

(b) Contour plot of percentages of endemic + potential endemic taxa in diatom communities (expressed as estimates of biovolume), on a matrix of disturbance vs. productivity indices. Contour lines are shaded in 20% increments from no shading (0%) though light (<20%) to black (>60%).

(c) Matrix of habitat types overlaid on the same axes as (b). Large dots are the locations of the mean disturbance and productivity score for each habitat type. The limits of standard deviations are enclosed in dotted lines. In (b) and (c), small dots indicate combinations of disturbance and productivity scores represented in the dataset.

widespread cosmopolitan taxa may be analogous to invasive species. In the words of Huston (1994), "… there is essentially no biological difference between the process of invasion and the process of colonization or recolonization of areas by native plants".

Methods

Sample collection and diatom analysis

Our data comprised diatom community composition and associated habitat information from samples collected from benthic freshwater habitats throughout New Zealand between 1999 and 2004, using standard collecting methods and habitat descriptors (Table I.1, Figure I.1). Permanent slides of diatom samples were prepared using standard methods (Round et al. 1990) and examined at 1000x under a Leica DMLB microscope. A visual assessment was made of the relative abundance by biovolume of each taxon on a scale from 1 (rare) to 8 (dominant) using the method described in Biggs and Kilroy (2000). This approach was appropriate for the present analysis because we were interested in the proportion of the diatom community accounted for by endemic taxa, rather than numbers of endemic vs. cosmopolitan taxa. Consistent effort was applied to each slide. Species identifications were made using a range of literature, and each species or morphospecies was assigned to one of five distribution categories, using published distribution information, except in the case of "distinctive potential endemics" and "possible endemics" (Table I.2). Approximate percentage biovolumes of each sample made up by diatoms in each distribution category were calculated from the sum of the scores for all taxa in that sample.

Table I.1. "Rules" for defining habitats from which diatom samples were collected.

Habitat	Definition	*n*
Bog	Rain-fed wetland, usually with *Sphagnum*	8
Lake	Larger waterbody, usually with inlet/outlet	29
Pool	Naturally occurring, small, shallow water body; temporary	25
River	High-order watercourse, >approx. 3 m wide	68
Rock seep/spring	Stable trickling water or seepage, or permanent splash zone of waterfall	13
Stream	Low-order watercourse, <approx. 3 m wide	102
Streamlet	Very small watercourse, <30 cm wide	18
Tarn	Small waterbody with no obvious inlet or outlet, usually high altitude; permanent (includes mire pools)	55
Wetland	Wetland associated with river, lake or groundwater (not ombrotrophic)	6

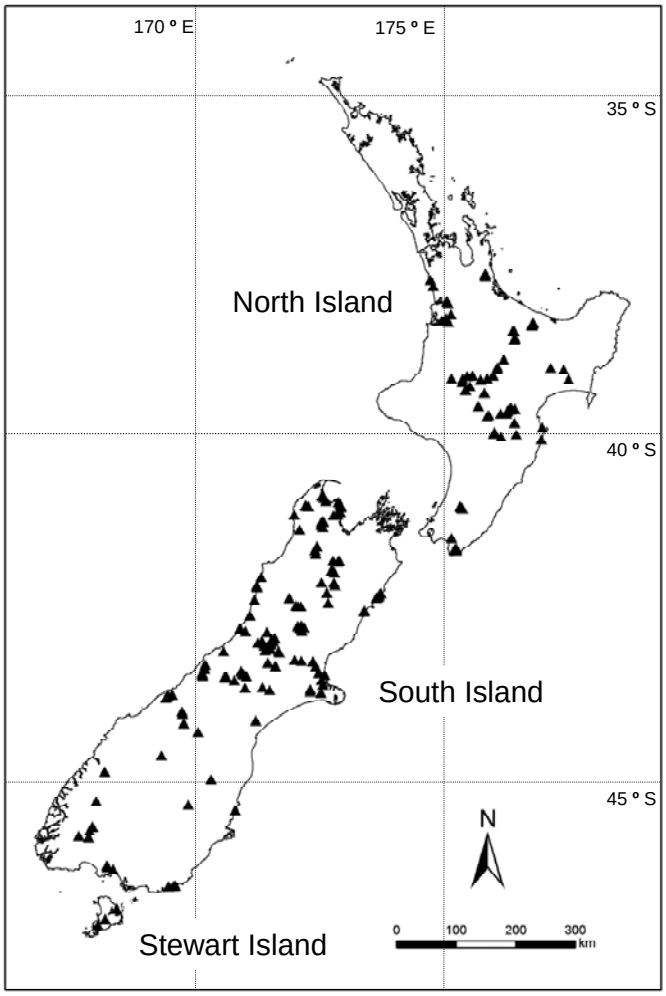


Figure I.2.
Locations of diatom sample collection sites

Table I.2. Diatom species distribution categories, and percentage of sites included in the present dataset at which they were observed.

Category	Explanation	No. species	Occurrence (% of sites)
Cosmopolitan	Morphologically indistinguishable, or with only subtle differences, from species stated in the literature to be cosmopolitan or occurring in the N. Hemisphere.	299	99
Southern Hemisphere	Stated in the literature to occur in the S. Hemisphere only; not recorded in the N. Hemisphere.	9	28
Endemic	Species described from New Zealand and/or Tasmania/Eastern Australia, and, to date, not recorded elsewhere to our knowledge.	9	18
Potential distinctive endemic	Distinctive morphospecies, usually similar to species already identified from Tasmania and E. Australia and to date not recorded elsewhere; also includes some distinctive, as yet undescribed, taxa.	39	24
Possible endemic	Resembling known cosmopolitan taxa but with sufficient morphological differences to preclude assignment to that taxon. Further study required.	71	26

As discussed by Hillebrand et al. (2001), correct and consistent species identifications in diatoms present some difficulties. First, there are a great many diatom species (Mann and Droop 1996). Second, morphologically similar taxa may represent genetically separate species (Mann et al 2004). Accordingly, we focussed mainly on morphologically distinctive taxa (the "endemic" and "distinctive potential endemic" classes in Table I.2) that are likely to have been long-separated in evolutionary terms from related taxa. Morphospecies included in the "possible endemic" class are less distinctive, but are assumed to have a high chance of having restricted distributions. It is acknowledged that the Southern Hemisphere and cosmopolitan classes may contain other endemic taxa belonging to clades of closely related species, which have a wide geographical distribution.

A further challenge is to demonstrate the true range size of an organism. Finlay et al. (2002) based their argument that almost all diatom species have a global distribution on the premise that it is impossible to prove that a species is *not* present in an area. The probability of finding taxa claimed to be endemic was assumed to be very small because such taxa are usually rare. In this study, endemics or distinctive potential endemics were not necessarily rare (see Appendix IA, page 35) therefore we have confidence that these taxa are not more widely distributed. Further, some recently described diatoms with apparently narrow distributions have been discovered in poorly studied, but widespread, habitats. For example, the distinctive, presumed endemic species *Eunophora oberonica* Vyverman and Hodgson was recorded from 36 of 71 small lakes and tarns in South Island and Stewart Island in 2001 (Vanhoutte et al. in press). Such species can also be abundant locally (Sabbe et al. 2001, Kilroy et al. 2006).

Measures of disturbance and productivity

To investigate diatom community composition relationships with disturbance and productivity, we developed estimates of these two parameters for each site. The *a priori* assignment of habitat type to each site (Table I.1) distinguished flowing-water and still-water environments. To further discriminate among sites we used a River Environment Classification (REC) developed for New Zealand (Snelder and Biggs 2002). The REC classifies stream segments using a hierarchy of controlling factors, viz., climate, geology, topography, and land cover. The classification covers the entire stream network of New Zealand, based on 1:50 000 topographical maps. Over 500,000 stream segments are defined, with an average spatial resolution of 0.75 km. Most of the diatom samples were collected over much shorter stream lengths, but the difference in scales should not affect this analysis. First, the REC defines segments that are uniform in character. Second, diatom community composition differences across microhabitats were accounted for by pooling multiple subsamples. In addition to the categorical information in the REC itself, detailed climate, landcover, geology and morphology information were available for each stream segment and its upstream catchment (Leathwick et al. 2003). These data could also be applied to still-water bodies

after defining their locations on the REC network. We selected appropriate variables from this dataset and used them to determine disturbance and productivity scores for each site.

The classical definition of disturbance in ecology is any physical perturbation that results in a loss of organisms much more rapid that their rate of replacement/recovery (Huston 1994). In the present analysis we follow Biggs et al. (1998) and consider disturbance in physical terms only (e.g., flow variability, wind-wave disruption, desiccation). Thus, the selected REC variables were surrogates for flood frequency, variability, and intensity, desiccation and wave disturbance (Table I.3). We assessed the relative availability of nutrients using data on catchment landuse and geology. In a study of 16 New Zealand rivers, Biggs (1995) found that, after flood frequency, mean periphyton biomass was best predicted from the proportions of catchments under intensive agricultural land use and occupied by alkaline rocks. Therefore, in the present analysis scores were derived from percentage of the upstream catchment under intensive agriculture, pastoral uses, and production forestry, with weightings applied to account for the greater relative impact of intensive agriculture on freshwater systems (Larned et al. 2004) (Table I.3). Lake productivity data (as total nitrogen and total phosphorus concentrations) for 7 of the 29 lakes in the present dataset showed a good correlation with the derived productivity scores ($R^2 = 0.750$; $P < 0.01$, $R^2 = 0.778$, $P < 0.01$, respectively), providing assurance that the scoring system was robust.

The resulting disturbance and productivity scores were scrutinized to ensure consistency with observations at each site. Once corrected, the ranked scores were used to generate categorical indices for disturbance (7 classes) and productivity (10 classes). Indexes were assigned to produce a linear relationship with the original estimates, with productivity square-root transformed to meet the requirements of a normal distribution.

Data analysis

We first focused on the percentage abundances of endemic plus distinctive potential endemic taxa (%end+dpend) as the main indicator of endemism at a site. If patterns of endemism in diatoms were consistent with our predictions (Figure I.1a), we expected to find negative relationships between the proportion of endemics in communities and both disturbance and productivity, with productivity showing the stronger relationship. Regression analyses on relative abundances vs. disturbance and productivity indices proved indeterminate because relative abundances varied widely within each group and in all cases included a large proportion of 100% values (for cosmopolitan taxa) or zeroes (for other distribution categories). Such patterns were expected because cosmopolitan taxa are known to dominate many diatom communities, and because of the influence of other unmeasured factors on community composition, e.g., recent disturbance history and season. An analogy is the polygonal nature of body size–abundance relationships. To define a relationship at the upper bound of the polygon, Blackburn et al. (1992) partitioned the independent

Table I.3. Selected New Zealand River Environment Classification variables used for derivation of disturbance and productivity scores.

Variable code	Description	Units	Range of values	Scoring system	Justification	Applied to:
Disturbance						
usArea	Total area of catchment upstream of the stream section	km^2	0 - >1000	Score of 0 – 5 assigned	Indicates potential size of large floods	Flowing water systems
usRainDays20	Mean number of days per month with rainfall >20 mm in catchment	days	0 - <7	Score of 0 – 7 assigned	Surrogate for flood-proneness of catchment	Flowing water systems
usAnRainVar	Coefficient of variation of annual catchment rainfall	mm	126 – 237	Score of 0 – 5 assigned	Indicates annual variability of floods and lake levels	All
segSlope	Average slope of REC stream section	ratio	0 – 37	Score of 0 – 7 assigned	Determines maximum water velocity and shear stress	Flowing water systems
Lake area	Approximate area of water body obtained from a range of sources including 1:50 000 maps	km^2	<0.0001->10	0 (<0.0001) to 10 (> 10)	Indicates potential for wave disturbance	Stillwater systems
Productivity						
LCDB30-32	% of catchment in high-intensity horticulture	%	0 – 100	Percentage value, weighted x3	Regular use of fertilizers and regular cultivation = high chance of impacts on water bodies	All
LCDB40	% of catchment in high-producing exotic grassland	%	0 – 100	Percentage value, weighted x2	Lower fertilizer use, but impacts of surface and groundwaters probable	All
LCDB41	% of catchment in low-producing grassland	%	0 – 100	Percentage value	Impacts from stock grazing; intermittent fertilizer	All
LCDB62-66	% of catchment in production forestry	%	0 – 100	Percentage value	Intermittent fertilizer, cultivation	All
usHard	Catchment average of hardness	ordinal scale	1 – 5	Scale reversed, converted to %	Natural inputs of nutrients from catchments with geology other than hard rock	All

variable (body size) into categories, then used least-squares regression to estimate the slope formed by the maximum *y*-value in each category. Since our independent variables (disturbance and productivity classes) were already categorical we followed this method rather than alternatives (e.g., Scharf et al. 1998), and ran linear regression analyses using community data over the 90th percentile of data in each disturbance and productivity group. A contour plot was used to illustrate the three-dimensional relationship between disturbance, productivity and relative abundance.

We then used ANOSIM (PRIMER v. 5.2.9, Clarke and Warwick 2001) to determine if there were significant differences in diatom communities in terms of all distribution categories among samples from the different disturbance and productivity groups. Somerfield et al. (2002) pointed out that ANOSIM lacks power when used to compare groups that represent a gradient, and may return a non-significant global result even when individual pairwise comparisons are significant. This was the case in the present analysis, therefore we ran the more appropriate global non-parametric test RELATE (PRIMER v. 5.2.9) in which a species similarity matrix is compared with a matrix of the distances between the grouping categories in gradient order. The non-parametric Kolmogorov-Smirnov (KS) test was used to identify any significant differences among habitat types in %end+dpend. (The KS test compares the cumulative distribution curves of two groups of samples.) We performed the same set of tests (except RELATE) using the *a priori*-defined habitat types. Finally, we generated bar graphs of numbers of samples containing diatom taxa in each distribution class versus disturbance and productivity indices and habitat type.

Other major environmental gradients that may affect diatom community composition, and possibly endemism/cosmopolitanism, include latitude and altitude, particularly through their correlations with temperature (both parameters) and human influence (altitude). Therefore, latitude and altitude (with altitude square-root transformed) were included in stepwise linear regressions on %end+dpend. ANOSIM was also run to test for significant differences among three altitude classes: low <500 m, medium 500-1000 m, high >1000 m. All analyses other than ANOSIM and RELATE were carried out using SYSTAT v. 10.

Results

Diatom communities

The analysis included 324 diatom samples, representing all areas of New Zealand and spread across a wide range of freshwater habitat types (Table I.1, Appendix IA, page 35) and altitudes (see below). We identified 427 taxa in 63 genera. Species composition across sites and habitats was extremely variable and reflected expected differences associated with substrate type and water chemistry, especially pH (Round et al. 1990). Just under 70% of all taxa (299) were placed in the cosmopolitan category. Although only nine taxa were assigned endemic status, a further 39 fell into the category of distinctive potential endemics and 71 were assessed as possible endemics.

The most common diatom species were *Cymbella kappii* Cholnoky and *Cocconeis placentula* Ehrenberg, which each occurred in 70 samples and together accounted for over 7% of the total relative abundance scores summed across all species and sites. *C. kappii* appears to have a Southern Hemisphere distribution (Foged 1979) and is classified as such in this analysis, along with eight other taxa (Table I.2). Other than *C. kappii*, taxa classified as having a Southern Hemisphere distribution formed a minor component of the total abundance. Known endemic taxa were found in 58 samples (18%, Table I.2). The most abundant of these were *Gomphoneis minuta* var. *cassieae* Kociolek and Stoermer (35 sites, mean relative abundance 5.3) and *Rhopalodia novae zealandiae* Hustedt (17 sites, 4.6). Distinctive potential endemics were observed in 79 samples, with *Kobayasiella* sp. 1 being the most abundant (26 sites, mean relative abundance 4.9). At 111 sites (34%) we recorded exclusively cosmopolitan communities, and only four sites did not contain cosmopolitan taxa. The dataset contained many rare taxa, with 186 species (almost 45%) recorded at a single site only, of which 119 were assigned a relative abundance score of 3 or less.

All taxa occurring in at least 10 sites are listed in the Appendix IA (page 35), along with the endemic taxa. The entire diatom dataset is accessible from NIWA's web-based Freshwater Biodiversity Information System database (fbis.niwa.co.nz, original master record = dia*) and voucher slides are archived in the NIWA diatom collection.

Relationships with habitat disturbance and productivity indices

Three-dimensional graphical representation of the %end+dpend in relation to both disturbance and productivity scores confirmed highest concentrations of these taxa in low disturbance environments, but spanning the whole range of productivities (Figure I.1b). Linear regression of the top 10% of %end+dpend values for each disturbance and productivity class showed a significant negative relationship with disturbance ($R^2 = 0.576$, $p < 0.001$) but not with productivity ($R^2 = 0.062$, $p = 0.081$). ANOSIM performed over disturbance groups using the five diatom distribution categories gave a non-significant global test, but the global RELATE test was significant (Table I.4). Separate pairwise comparisons showed that the greatest differences in community composition (as indicated by highest R values and $P < 0.05$) were between the two lowest disturbance groups and some of the higher categories (Table I.4). Cumulative distributions of %end+dpend for disturbance indices of 1 and 2 were more different from those of all other disturbance groups, than from each other (Table I.5a). In this KS test, probabilities exceeded Bonferroni-corrected levels but seven significant results out of 21 pairwise tests suggests biological significance particularly as the results reflect those based on all five distribution groups (Table I.5). Examination of the cumulative distribution curves confirmed that the differences were largely a result of higher %end+dpend in the low-disturbance groups. Conversely, across the 10 productivity groups global ANOSIM and RELATE indicated random community composition in terms of the distribution categories (Table I.4), and there were fewer differences in %end+dpend across groups (Table I.5b).

Table I.4. Differences in diatom community composition (in terms of diatom distribution classes) among disturbance and productivity groups, altitude groups, and habitat types. Results from the global test RELATE are reported (ρ) for the disturbance and productivity index gradients, followed by pairwise comparisons in ANOSIM (R). For altitude and habitat, global and pairwise ANOSIM results are shown. Only significant pairwise comparisons (P < 0.05) are listed. * indicates Bonferroni-corrected significance. n.s. = not significant.

Factor	Pairwise comparison	Statistic (ρ or R)	P
Disturbance index	**Global**	**ρ = 0.034**	**0.019**
	1 x 5	R = 0.053	0.001*
	2 x 3	R = 0.102	0.001*
	2 x 4	R = 0.119	0.002*
	2 x 5	R = 0.202	0.001*
	2 x 6	R = 0.091	0.002*
Productivity index	**Global**	**ρ = 0.009**	**0.315 n.s.**
Altitude	**Global**	**R = 0.045**	**0.002**
	1 x 2	R = 0.035	0.029
	1 x 3	R = 0.085	0.001*
	2 x 3	R = 0.036	0.002*
Habitat	**Global**	**R = 0.086**	**0.001**
	Bog vs. lake	R = 0.305	0.023
	Bog vs. river	R = 0.467	0.001*
	Bog vs. stream	R = 0.405	0.004
	Bog vs. streamlet	R = 0.365	0.007
	Bog vs. rock seep / spring	R = 0.206	0.029
	Tarn vs. river	R = 0.177	0.001*
	Tarn vs. stream	R = 0.156	0.001*

Proportions of sites with endemic + distinctive potential endemic and possible endemic taxa were highest in low-disturbance environments and vice-versa (Figure I.3a). There was no clear trend across productivity indices although proportions of sites containing endemic + distinctive potential endemic taxa were highest for productivity index = 1 (Figure I.3b).

Diatom community composition (by distribution category) was significantly related to altitude (Table I.4), and this was reflected in variations in the occurrences of different diatom over the three altitude groups (Figure I.4). However, stepwise linear regression including disturbance, productivity, altitude and latitude confirmed that disturbance and productivity (in that order) were the most important factors accounting for variability in %end+dpend. Total variance explained was very low ($R^2 = 0.233$), reflecting the great variability in the dataset.

Table I.5. Kolmogorov-Smirnov (KS) statistics (*D*) for differences in relative abundances of endemic + distinctive potential endemic diatoms (%end+dpend) among (a) disturbance classes, (b) productivity classes, and (c) habitats. Bold type indicates a significant difference between groups with P<0.05; * P<0.005; **Bonferroni-corrected significance.

(a)	1	2	3	4	5	6
2	0.163					
3	0.234	0.295				
4	0.256	**0.399***	0.129			
5	**0.299***	**0.365***	0.101	0.074		
6	**0.282**	**0.343**	0.095	0.092	0.074	
7	**0.345**	**0.402**	0.135	0.104	0.079	0.119

(b)	1	2	3	4	5	6	7	8	9
2	**0.262**								
3	**0.310**	0.177							
4	**0.336**	0.116	0.105						
5	0.258	0.055	0.148	0.142					
6	**0.350**	0.164	0.130	0.130	0.166				
7	0.289	0.145	0.185	0.086	0.185	0.140			
8	**0.467***	0.311	0.170	0.227	0.281	0.165	0.269		
9	**0.330**	0.161	0.079	0.069	0.132	0.076	0.138	0.189	
10	0.370	0.222	0.114	0.106	0.193	0.130	0.143	0.162	0.099

(c)	Bog	Lake	Pool	River	Stream	Streamlet	Tarn	Rock seep/spring
Lake	0.362							
Pool	0.300	0.102						
River	0.382	0.089	0.146					
Stream	0.392	0.095	0.155	0.069				
Streamlet	0.389	0.123	0.218	0.075	0.085			
Tarn	0.255	**0.355**	0.287	**0.397****	**0.397****	**0.469***		
Rock seep/spring	0.346	0.156	0.246	0.140	0.101	0.098	**0.464**	
Wetland	0.333	0.322	0.267	0.373	0.382	0.444	0.433	0.436

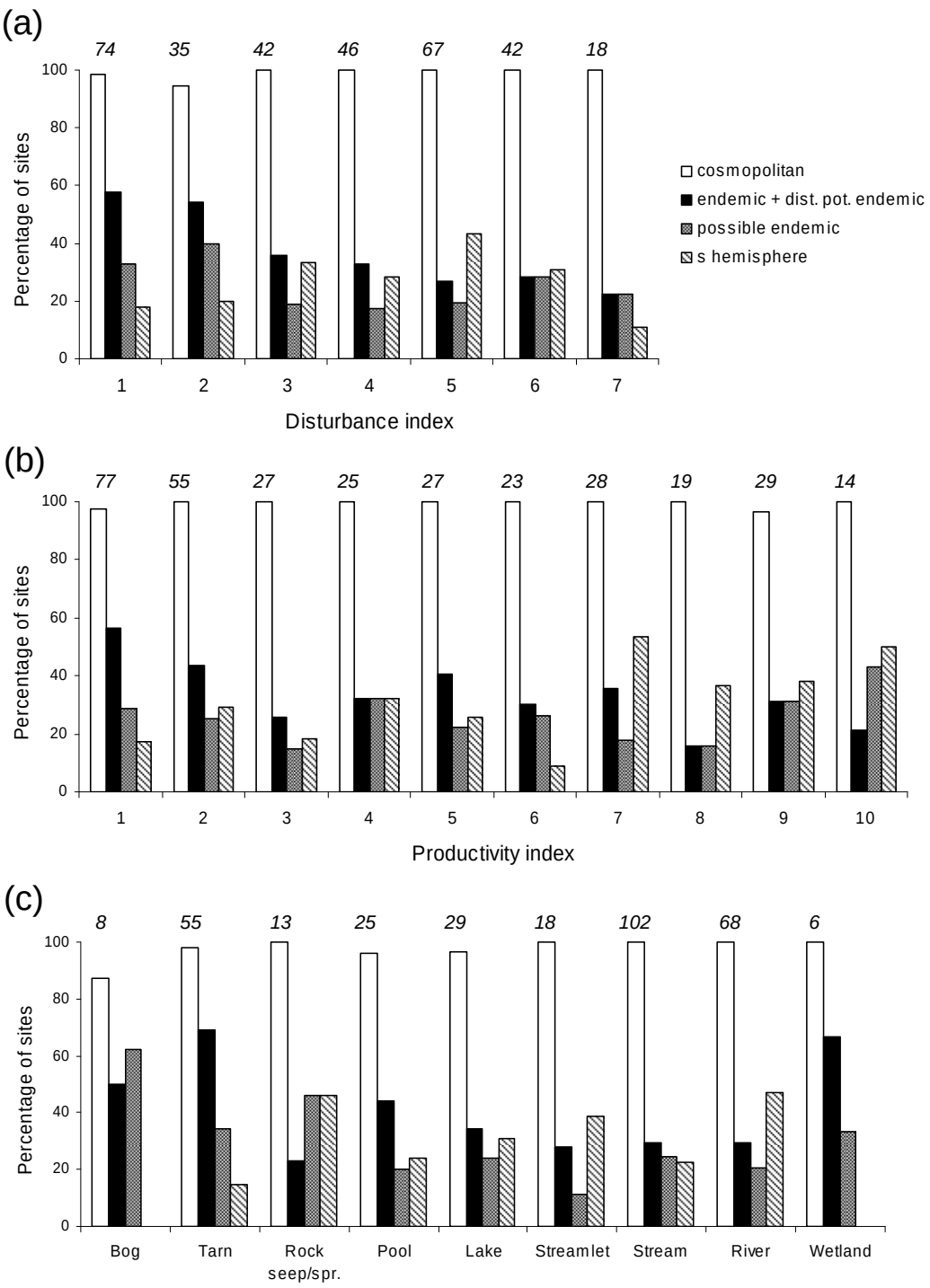


Figure I.3. Percentages of sites containing diatom taxa classified into cosmopolitan, endemic + distinctive potential endemic, possible endemics, and Southern Hemisphere, according to: (a) relative degree of disturbance, on an index of 1 (low disturbance) to 7 (high disturbance); (b) relative productivity, on an index of 1 (low productivity) to 10 (high productivity); (c) habitat type (see Table I.3 for definitions). Numbers of sites are shown in italics above each index or habitat category.

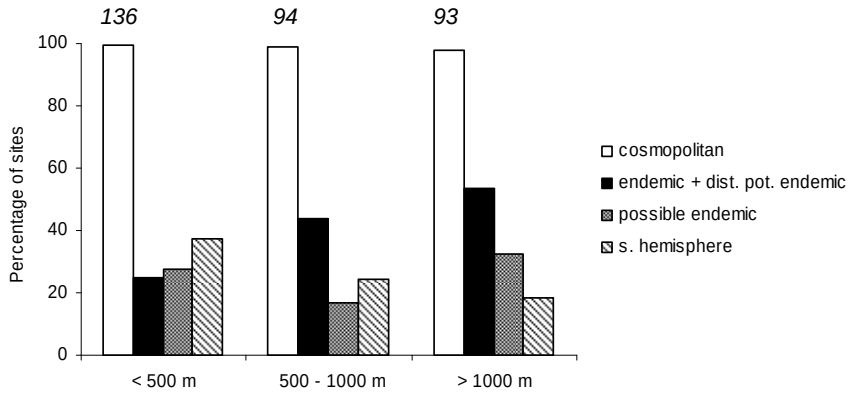


Figure I.4. Percentages of sites within three altitude categories containing diatom species classified as in Figure I.3. Number of sites is shown in italics above each altitude category.

Relationships with habitat type

Communities from bogs differed from those in lakes and all running water habitats, and those in tarns differed from rivers and streams, with the strongest difference between communities in tarns and rivers (Table I.4). In KS tests cumulative distribution curves for %end+dpend were significantly different between tarns and all other habitats except bogs, pools and wetlands (Table I.5c). Again this was due to samples from tarns containing higher %end+dpend (curves not illustrated). Endemics + distinctive potential endemics and possible endemic species occurred more frequently at sites classified as bogs, tarns and wetlands than in other habitat types (Figure I.3c).

Discussion

Given existing impressions of a largely cosmopolitan diatom flora in New Zealand (approximately 2.3% endemic taxa, Harper et al. 2005), the occurrence of documented endemic taxa in less than 20% of samples was not surprising. More unexpected was our finding of taxa classified as distinctive potential endemics or possible endemics in over 40% of sites, with representatives ranging widely in abundance and covering all habitat types (Figure I.3). Both graphically and statistically, diatom communities from tarns and bogs emerged as distinctive, with higher proportions of endemics and distinctive potential endemics, compared to communities in lakes, rivers and streams.

The results of the present analysis can be readily reconciled with the DEM explanation (Figure I.1a). Overlaying the *a priori* habitat types on the disturbance vs. productivity matrix (Figure I.1c) confirms that tarns and bogs predominantly fall into the low-disturbance, low-productivity area, where DEM theory predicts most endemics to occur. However, while Huston (1994) emphasised the association between endemic plant species and low productivity environments, our data showed a strong tendency for endemic and distinctive potential endemic taxa to occur in communities from

low-disturbance environments, regardless of productivity, although endemic taxa (particularly *Gomphoneis minuta* var. *cassieae*) did occur in sites with moderate to high disturbance scores. In view of the strong links between disturbances, invasions, and loss of endemics (Thomson 2005), we would expect low disturbance to be more critical for the maintenance of endemic taxa than implied in Huston (1994). The discrepancy between our results and predicted patterns may also arise from application of a theory developed mainly using terrestrial organisms to an aquatic group. Huston stated: "disturbances are critical for the invasion of productive habitats…", and "There are few, if any, examples of invading species becoming dominant in undisturbed, productive ecosystems." He also stressed that that most successful invasions into productive landscapes are associated with gross man-made disturbances, such as agriculture and urbanisation, and that, globally, nearly all such productive terrestrial environments have been exploited by humans. Highly productive aquatic environments, on the other hand, are likely to be products of human disturbances on land, through agricultural runoff and sedimentation (Larned et al. 2004) and may not have been physically disturbed. In addition, underlying geology makes some systems naturally productive (Biggs 1995). In the present analysis, we found several endemic and potential endemic taxa dominating the diatom communities in high-productivity North Island lakes and rock seeps. In all cases, the high productivity score resulted from geological as well as land-use factors (Table I.3), suggesting naturally high productivity at these sites. In other words, we suggest that enhanced productivity in undisturbed, naturally productive aquatic habitats may have little effect on the persistence of endemic taxa that are already thriving in those environments. This is in agreement with the results of a review of freshwater algal endemism in Australia (Tyler 1996) in which the author suggests that endemic algal species in Australia fall into two groups: fragile endemics, generally restricted to pristine, undisturbed lakes; and robust endemics, which have wider distributions, and tolerate a wide range of water quality oligotrophic to eutrophic. We propose that the endemic taxa found in the high-productivity North Island sites are analogous to Tyler's robust endemics. The general patterns of endemism found in this analysis were also largely consistent with that found in a study by Burke and Grime (1996) and discussed by Huston (2004), in which the dominance of invasive plant species was assessed in relation to disturbance and productivity. In that study, levels of invasive species were low across all productivity levels when disturbance intensity was low, with minimum levels in high productivity conditions (Fig. 4 in Huston 2004), i.e., roughly the mirror image of the patterns shown in Figure I.1b in the present paper.

The DEM explanation for the maintenance of endemic taxa arising from habitat characteristics at least partly explains the observed coexistence of endemic and cosmopolitan diatom taxa in New Zealand freshwaters, if widespread cosmopolitan taxa are considered analogous to invasive taxa. Such an environmental explanation for maintenance of species assemblages also concurs with the more recent theory on invasibility (Davis et al. 2005). Further analogies may be drawn from studies on vascular plants. For example, Gilbert and Lechowicz (2005) found that species invading stable,

old-growth forests did not displace native species, regardless of resource supply or to proximity to human-disturbed areas. They concluded that “exotic species with niche requirements not well-represented in the native flora can colonize …. with little resistance or consequence for native species”. In that case, the exotic species were not considered to be aggressive invaders. On the other hand, habitat modification through disturbance has been shown to both directly impact on native species, and to facilitate dominance by invasive species (MacDougall and Turkington 2005). In a review of the mechanisms for the coexistence of many species in tropical forests, Wright (2002) also found strong support for niche segregation one of the major mechanisms for maintenance of high diversity and many rare species. Small-scale environmental heterogeneity has been shown to be linked to species patchiness in benthic stream algae (Passy 2001), suggesting a similar coexistence mechanism in these aquatic microorganisms.

An analogy between widespread cosmopolitan taxa and invasive species has been implied previously, with the suggestion that many cosmopolitan diatom taxa have wide distributions because of human-mediated dispersal, and that a core of 150-200 taxa may “occur across great ecological and geographical space that has been influenced by urbanization” (Kociolek and Spaulding 2000). The distinction between imported or invasive species and naturally cosmopolitan taxa does not directly affect the present analysis, but does highlight the issue of the true extent of cosmopolitanism in the New Zealand diatom flora. For example, there is no doubt that the invasive diatom *Didymosphenia geminata* (Lyngbye) A. Schmidt is a recent arrival in New Zealand (Kilroy 2004). This species was not known in New Zealand during the period of sample collection for the present study.

In conclusion, this study has identified patterns in endemism in freshwater diatoms on the basis of measurable habitat attributes. Although we classify environmental conditions at a relatively coarse (landscape) scale, we confirm that stable, low-productivity environments, largely as predicted by the DEM, appear most likely to harbour endemic diatom taxa. The fact that diatoms conform to similar environment-based patterns in the occurrence of endemism as observed in macroscopic organisms supports the view that ubiquity in these micro-organisms is not a general rule (Finlay et al. 2002). In terms of habitat types, tarns and bogs are identified as highly likely candidates for endemism in diatoms, generally in the form of as yet undescribed taxa. Surprisingly, it appears that endemic diatom taxa may persist in stable habitats even within productive, agricultural landscapes, and we suggest that these sites may also be naturally productive.

Appendix IA

List of all diatom taxa occurring in 10 or more sites, and all taxa classified as endemic, with identification references. KLB = Krammer and Lange-Bertalot (1991 – 1997). Distribution status: sh = Southern Hemisphere, cos = cosmopolitan, end = endemic, dpend = distinctive potential endemic, p_end = possible endemic (see Table I.1 for further details).

Taxon	Reference	Distr. group	No. sites
Cymbella kappii Cholnoky	Foged 1979	sh	70
Cocconeis placentula Ehrenberg	Foged 1979, KLB	cos	70
Planothidium lanceolatum (Brebisson) Round & Bukhtyarova	Round & Bukhtiyarova	cos	65
Encyonema neogracile Krammer	Foged 1979 (= *Cymbella gracilis*), Krammer 1997	cos	56
Encyonema minutum (Hilse in Rabenhorst) D.G. Mann	Foged 1979 (= *Cymbella minuta*), Krammer 1997	cos	51
Diatoma heimale var. *mesodon* (Ehrenberg) Grunow	Foged 1979, Patrick and Reimer 1966	cos	50
Tabellaria flocculosa (Roth) Kutzing	KLB	cos	43
Fragilaria vaucheriae (Kützing) Petersen	Foged 1979	cos	41
Encyonema silesiacum (Bleisch in Rabenhorst) DG Mann	Krammer 1997a	cos	38
Synedra ulna (Nitzsch) Ehrenberg	Patrick and Reimer 1966	cos	38
Achnanthidium minutissimum (Kützing) Czarnecki	Round and Bukhtiyarova 1996	cos	35
Gomphoneis minuta var. *cassieae* Kociolek and Stoermer	Kociolek and Stoermer (1988)	end	35
Epithemia sorex Kützing	KLB	cos	35
Gomphonema parvulum Kützing	Foged 1979, KLB	cos	32
Rossithidium pusillum (Grunow) Round & Bukhtiyarova	Round and Bukhtiyarova 1996	cos	32
Fragilaria capucina Desmazieres	Foged 1979, KLB	cos	31
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot	KLB	cos	30
Frustulia rhomboides (Ehrenberg) De Toni	KLB	cos	29
Navicula lanceolata (C. Agardh.) Ehrenberg	KLB	cos	29
Navicula radiosa Kützing	KLB	cos	29
Kobayasiella sp. 1	Vanhoutte et al. 2004	dpend	26
Gomphonema clavatum Ehrenberg	KLB	cos	25
Gomphonema kobayasii Kociolek & Kingston	Kociolek and Kingston 1999	cos	21
Cymbella cymbiformis Agardh	KLB	cos	21
Synedra ulna var. *contracta* Oestrup	Patrick and Reimer 1966	cos	19
Frustulia vulgaris (Thwaites) De Toni	KLB	cos	19
Frustulia magaliesmontana Cholnoky	Foged 1979, Fallu et al. 2000	cos	18
Pinnularia microstauron (Ehrenberg) Cleve	Krammer 1992	cos	18
Gomphonema truncatum Ehrenberg	KLB	cos	18
Brachysira brebissonii Ross	Lange-Bertalot and Moser 1994	cos	17
Synedra rumpens Kützing	Patrick and Reimer 1966	cos	16
Rhopalodia novae zealandiae Hustedt	Schmidt et al. 1874 – 1959, also see Foged 1979	end	16
Navicula cryptocephala Kützing	KLB	cos	16
Nitzschia linearis (Agardh ex W. Smith) W. Smith	KLB	cos	16
Nitzschia palea (Kützing) W. Smith	KLB	cos	15
Eunotia bilunaris var. *mucophila* Lange-Bertalot & Norpel	KLB	cos	15
Rossithidium petersenii (Hustedt) Round & Bukhtiyarova	Round and Bukhtiyarova 1996	cos	14
Cyclotella stelligera Cleve & Grunow	KLB	cos	14
Sellaphora pupula (Kützing) Mann	species complex: Mann 1989, Mann et al 2004	cos	14
Gomphonema acuminatum (O. Muller) Cleve	KLB	cos	14
Planothidium frequentissimum (Lange-Bertalot) Round & Bukhtiyarova	Round and Bukhtiyarova 1996	cos	13
Brachysira procera Lange-Bertalot	Lange-Bertalot and Moser 1994	cos	13
Neidium ampliatum (Ehrenberg) Krammer	KLB	cos	13
Navicula gregaria Donkin	KLB	cos	13
Eunotia exigua (Brebisson) Rabenhorst	KLB	cos	13
Nitzschia dissipata (Kützing) Grunow	KLB	cos	13
Navicula capitatoradiata Germain	KLB	cos	12
Pinnularia subcapitata Gregory	KLB, Krammer 1992	cos	12

Taxon	Reference	Distr. group	No. sites
Achnanthes subatomoides (Hustedt) Lange-Bertalot & Archibald	Bukhtiyarova and Round 1996, KLB (as *Achnanthes subatomoides*)	cos	12
Brachysira neoexilis Lange-Bertalot	Lange-Bertalot and Moser 1994	cos	12
Gomphonema gracile Ehrenberg		cos	12
Frustulia crassinervia (Brebisson) Lange-Bertalot & Krammer	Lange-Bertalot and Metzeltin 1996	cos	11
Brachysira wygaschii Lange-Bertalot	Lange-Bertalot and Moser 1994	cos	11
Eunotia incisa Gregory	KLB	cos	11
Frustulia sp. 6	Flower 2005	dpend	11
Adlafia sp.	Moser et al. 1998, Rumrich et al.	dpend	11
Pinnularia cf. *subcapitata* var. *elongata* Krammer	Krammer 1992	p_end	11
Eunotia rhomboidea Hustedt	KLB	cos	11
Synedra ulna var. *biceps* (Kützing) v. Schonf.	Foged 1979	cos	11
Nitzschia amphibia Grunow	KLB	cos	11
Surirella linearis W. Smith	KLB	cos	11
Epithemia adnata (Kützing) Brebisson	KLB	cos	11
Brachysira sp. 1	see Lange-Bertalot and Moser 1994	dpend	10
Gomphonema parvulum var. *lagenula* (Grunow) Hustedt	KLB	cos	10
Gomphonema angustum Agardh	KLB	cos	10
Gomphonema minutum (Agardh) Agardh	Kociolek and Kingston 1999	cos	10
Eunotia implicata Norpel, Lange-Bertalot & Alles	KLB	cos	10
Cymbella naviculiformis (Auerswald) Cleve	KLB	cos	10
Surirella angusta Kützing	KLB	cos	10
Hantzschia amphioxys (Ehrenberg) W.Smith	KLB	cos	10
Actinella aotearoia	Sabbe et al. 2001	end	3
Fragilariforma cassieae Kilroy & Bergey	Kilroy et al. 2003	end	3
Eunophora oberonica Vyverman & Hodgson	Vyverman et al. 1998	end	3
Pinnularia segariana Foged	Foged 1979	end	1
Encyonema tasmaniense Krammer	Krammer 1997b	end	1
Amphora bergrennii Cleve (= Eunophora sp. 1)	Vyverman et al. 1998	end	1
Fragilariforma rakiuriensis	Kilroy et al. 2003	end	1

2.II Benthic diatom communities in subalpine pools in New Zealand: relationships to environmental variables

Introduction

Diatom communities respond quickly to environmental changes because of their short life-cycles, rapid dispersal and colonisation and the large number of species with differing tolerances to physical and chemical variables (Lotter et al. 1999), notably pH (Battarbee et al. 1999). Consequently diatoms are well-established tools both for monitoring present changes in water condition (Stevenson and Pan 1999; Winter and Duthie 2000), and for tracking past environmental changes inferred from communities preserved in sediments (Moser et al. 1996; Smol and Cumming 2000). High-latitude and high-altitude aquatic ecosystems have been identified as being especially sensitive to environmental changes (Pienitz and Smol 1993; Vincent and Pienitz 1996; Sommaruga-Wograth et al. 1997; Smol and Cumming 2000), and over the past 10-15 years there have been numerous studies to establish diatom community composition and environmental preferences in lakes and ponds in the Northern Hemisphere, especially in arctic regions (e.g. Douglas and Smol 1995; Fallu et al. 2000; Laing and Smol 2000; Lim et al. 2001; Michelutti et al. 2003). In the Southern Hemisphere, however, equivalent information is still relatively sparse, though comprehensive data are available for Tasmanian and Antarctic lakes (Vyverman et al. 1995, Verleyen et al. 2003 and references therein).

In New Zealand, small lakes, tarns and mire pools are characteristic features of alpine and subalpine landscapes, especially in the Southern Alps, South Island. Recent estimates from the NZMS 1:50 000 map database (Land Information New Zealand) indicate that in the South Island there are over 7500 small lakes and ponds (<10 ha area) located at over 600 m a.s.l. (H. Hurren, pers. comm.). Despite their prominence in the landscape and potential biodiversity and conservation values, small subalpine/alpine waterbodies have been the focus of surprisingly few studies. Taxonomic work over the past few years in the Australasian region suggests that these habitats support significant numbers of diatom taxa that appear to be endemic to the Southern Hemisphere (Vyverman et al. 1997, 1998, Sabbe et al. 2001, Kilroy et al. 2003 [VII]), and for which only general autecological data are available. Thus, to understand the biodiversity of high-altitude diatom communities and to exploit their value as indicators of environmental changes and of natural habitats in this region (Kociolek and Stoermer 2001), more information is required on community composition and the environmental conditions that influence individual taxa. Data from unmodified areas are especially important in order to provide a reference point in future studies of both human impacts and climate change (Battarbee et al. 1997).

Analysis of data from a survey in January 2001 of 71 small lakes, tarns and mire pools in predominantly unimpacted South Island catchments at altitudes up to 1520 m a.s.l. characterised

their general limnology and benthic diatom community composition at the genus level (K. Vanhoutte, pers. comm.). The present investigation focuses on a system of subalpine pools, which includes two of the sites sampled in the earlier survey. The aims of this more detailed study were: 1) to characterise diatom community composition in a typical unimpacted subalpine mire pool complex in New Zealand, including recognition of potential Southern Hemisphere endemic taxa; 2) to investigate the importance of a range of environmental variables in explaining the distributions of diatom communities and species over a relatively small area without the confounding large-scale influences of climate and geology; and 3) to identify diatom species that could potentially be used as indicators of specific water chemistry conditions in these environments. We also aimed to obtain preliminary information on the environmental preferences of species in the known endemic genus *Eunophora* (Vyverman et al., 1998).

Site description

The investigation was conducted in a wetland area approximately 1000 m x 200 m occupying a shelf on the northern flank of Bealey Spur (43° 02′ S, 171° 35′ E) near Arthur's Pass, South Island, New Zealand, at about 1030 m a.s.l. (Figure II.1). The locality is typical of the many small tarn/mire pool complexes that occur throughout the Southern Alps, generally in basins originally shaped by glaciation (Lowe and Green 1987). Bealey Spur lies to the east of the main divide of the Southern Alps and runs roughly east to west. Basement geology is greywacke (hard siliceous sedimentary rock laid down in the Jurassic/Triassic), which underlies much of the northern section of the Southern Alps. Acid "brown soils" are typical of the eastern ranges of this part of the Southern Alps (Morgan 2001), however, soils in the vicinity of the pools sampled were largely organic. Annual rainfall in the area is approximately 2000 mm.

Until the late 1970s Bealey Spur, including the wetland area, was pastoral leasehold land and there was low-density sheep grazing in the adjacent subalpine tussock land up to about 1800 m a.s.l. Nevertheless, there is little evidence of attempts to "improve" the land for grazing by planting exotic grass and herbaceous species, as was common practice in other subalpine grassland areas in New Zealand. The remains of *Nothofagus* stumps around the wetland suggest forest burning in the past. A large fire in the 1880s affected the spur immediately to the east, but there has been no significant burning in the area since then (McLeod 1974). In 1978, the land was transferred to the (now) Department of Conservation, which provides protection against any further development. A board-walked track crosses the eastern edge of the wetland area (Figure II.1). Other than this, the area is largely unimpacted by human activities and therefore a suitable location for a baseline study of benthic algal communities.

In the wetland itself, a deep (>1.5 m), relatively large tarn at the western end is flanked by a series of smaller, shallow pools. Elevation falls about 20 m towards the boardwalk, where there are numerous pools within a predominantly waterlogged area. All the pools have well-defined vertical

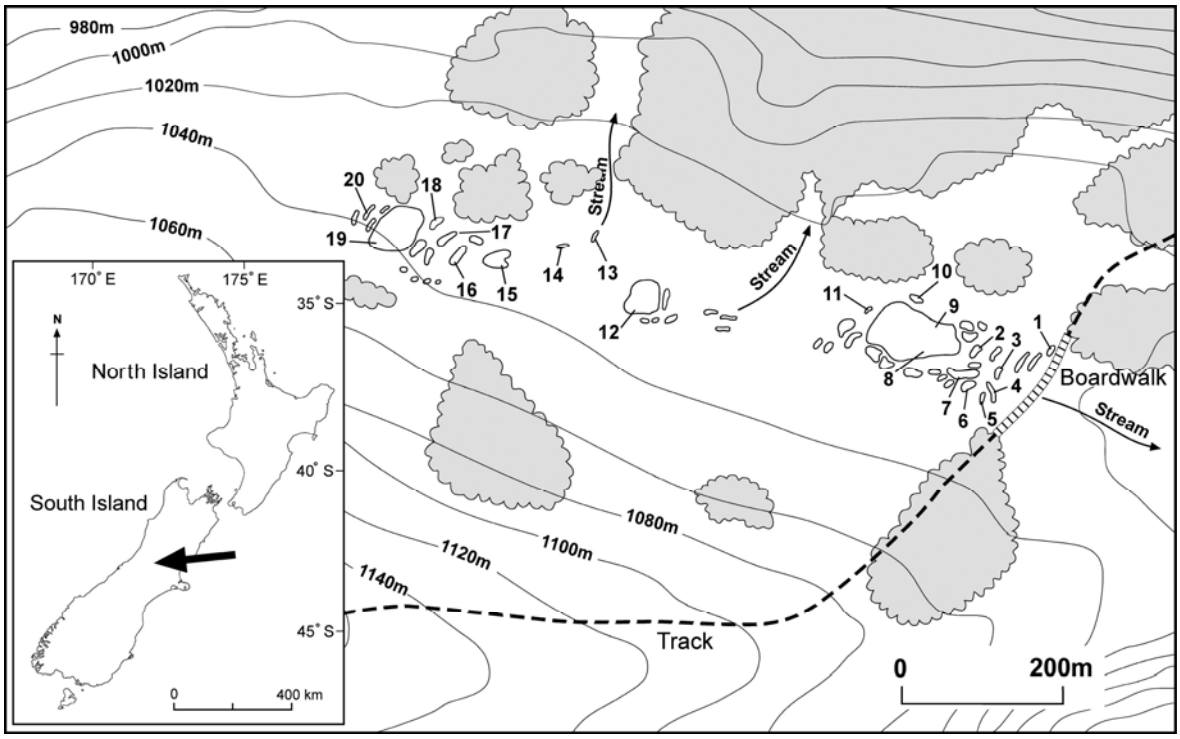


Figure II.1. Sketch map of the study site at Bealey Spur wetland area, near Arthur's Pass, South Island, New Zealand, showing general landscape features and relative locations of the 20 sampling sites. Note that not all pools in the area are shown.

peat margins and water depth is typically <50 cm. Three small streams drain the wetland, one to the east and two to the north (Figure II.1). Vegetation is a mixture of tussock (*Chionochloa* spp.) and subalpine shrubs (*Hebe* spp.) in well-drained areas on the flanks of the wetland, giving way to tussock species mixed with typical alpine wetland species including *Empodisma minus*, *Dracophyllum* sp., *Gleichenia dicarpa*, *Lycopodium* sp. and *Sphagnum* sp. The area is more or less on the tree line, with large stands of mountain beech (*Nothofagus solandri* var. *cliffortioides*) on the lower slopes to the north of the wetland, and scattered patches on the higher ground to the south. The substrate in most pools comprises soft algal and other organic detritus ranging in depth from a few millimetres to 1.5 m or more. The thinnest organic layers are in small pools directly connected to streams. Deeper organic substrates resemble those described for mire pools elsewhere (Foster and Fritz 1987). In some pools the top ~10 mm is consolidated into a firm cyanobacterial mat, laminated into an upper red-brown layer, with a bright green layer beneath, similar in appearance to microbial mats described from Antarctica (Vincent et al. 1993, Sabbe et al. 2004).

Methods

Algae

Qualitative samples of benthic algae were collected from 20 pools on the same day in the early austral spring 2001. Sites were selected to cover the whole of the wetland area and to include a wide range of pool size. All samples were from water depths between 0.2 and 0.4 m. Two small

pools (sites 13 and 14) were directly connected to the western stream draining the wetland to the north. No other site had any obvious surface inflow or outflow. Samples were taken approximately 0.5 m from the pool margins. At each site 4 or 5 small cores (10-mm diameter) from the top 15 mm of substrate were combined into a single sample and preserved in glutaraldehyde (final concentration of 2.5%) within 6 h of collection. Subsamples were examined under an inverted microscope at magnifications up to x400. A scale of 1 (rare) to 8 (dominant) was used to assess the relative abundance of major groups of algae and other material using the method described in Biggs and Kilroy (2000). The groups were: cyanobacteria, fine trichomes < 5 μm diameter (cf. *Leptolyngbya* spp.); coarse trichomes > 7-10 μm diameter (e.g. *Tolypothrix*, *Hapalosiphon*); colonial unicellular cyanobacteria; desmids; diatoms; green filamentous algae; organic detritus; inorganic material (silt/sand). Scores assigned to diatoms are an estimate of the relative abundance of living cells (i.e. containing chloroplasts).

Further subsamples were oxidised in concentrated sulphuric acid followed by hydrogen peroxide to remove all organic material, then rinsed in distilled water. Drops of the resulting suspension of diatoms were dried onto coverslips and mounted onto glass slides using Naphrax (Northern Biological Supplies, UK). Slides were examined at x1000 on a Leica DMLB microscope with differential interference contrast optics, and counts made across transects. At least 600 valves were counted per sample. Diatoms were identified to species level where possible, using a range of texts (see Table II.1). Where no satisfactory identification could be made, species were assigned numbers (e.g. *Kobayasiella* sp. 1) and photographed for further investigation (Zeiss Axiocam mounted on a Leica DMLB, and Leica S440 scanning electron microscope). Morphospecies were placed in one of the following categories: 1) indistinguishable from species described and recorded from the Northern Hemisphere (i.e. likely to be cosmopolitan); 2) known species recorded to date only in the Southern Hemisphere; 3) closely resembling a known species; 4) genus only, unknown species.

Environmental variables

Water pH, conductivity and temperature were measured in the field using a TPS WP-81 meter (TPS Pty Ltd, Australia). Water samples were collected into acid-cleaned polyethylene bottles and sub-samples filtered in the field for subsequent analyses of nutrients, dissolved organic carbon (DOC), and major anions and cations. In the laboratory, a subsample was filtered prior to measuring absorbance at 440 nm using the method of Davies-Colley et al. (1993). This provides a convenient measure of the UV-absorbing yellow colour in water caused by dissolved humic substances, referred to here as gilvin (g_{440}) but also known as Gelbstoff or yellow substance (Yacobi et al. 2003). Nitrate-nitrogen, ammonium, dissolved reactive phosphorus (DRP), total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were determined on a Technicon 2 Auto-analyser, after UV irradiation in respectively alkaline or acidic, conditions (Downes 2001). Dissolved organic nitrogen (DON) and phosphorus (DOP) were determined as TDN minus (NH_4 +

nitrate N), and TDP minus DRP, respectively. Analyses for major ions (K, Na, Ca, Mg, Si, Cl, SO_4) and DOC were undertaken using standard methods (APHA 1998) at the Landcare Research Environmental Chemistry Laboratory, Palmerston North.

Numerical analyses

The diatom dataset was square-root transformed in order to downweight the effects of dominant taxa (>20% in many samples) (Laing and Smol 2000). All of the environmental variables except water depth, pH, DOC, gilvin and Na had skewed distributions and were log-transformed for subsequent analyses. A Pearson correlation matrix with Bonferroni-adjusted probabilities (SYSTAT, v. 10) identified several significantly correlated sets ($P < 0.05$). Redundant variables were selected by running preliminary BIO-ENV analyses (see below) for each and retaining the variables that yielded the highest rank correlation with the diatom dataset. The following variables were eliminated: DOC (correlated with gilvin), DRP, NH_4, TDN, DON (all correlated with TDP), Ca (correlated with conductivity), Mg (correlated with Ca).

Relationships between diatom community composition and environmental variables were explored using the BIO-ENV procedure in the University of Plymouth's program PRIMER (Clarke and Warwick 2001). BIO-ENV was considered to be suitable for exploring the present dataset because of the small number of samples from a restricted area. The procedure requires no prior assumptions about the nature of the relationships (i.e., linear or unimodal) of biota to environmental variables (Clarke and Ainsworth 1993), and therefore was expected to produce a realistic result within a low range of environmental conditions. BIO-ENV compares a similarity matrix of the biotic data with similarity matrices of all combinations of associated environmental data and computes a Spearman rank correlation coefficient ρ_s for each combination. The coefficient ranges from –1 (ranks in complete opposition) to 1 (ranks in complete agreement). Matrices were constructed using Bray Curtis similarities for the diatom data, and normalised Euclidean distance for the environmental dataset. The environmental variables identified as having the closest correlations with the biotic data can be visualised by comparing non-metric multidimensional scaling (MDS) plots of the two datasets. MDS plots are based on matrices of ranked similarities and configure the sites in a specified number of dimensions (usually two) such that similar sites are close together and dissimilar sites are far apart. Values of $\rho_s > 0.8$ generally produce a close visual match, providing that the *stress* for both plots is low (Clarke and Ainsworth 1993). Stress is a measure of how well the data are represented in the number of dimensions specified: values < 0.1 indicate a good representation; values >0.1 and <0.2 are acceptable (Clarke and Warwick 2001). Note that currently there is no means in the BIO-ENV procedure of establishing whether a relationship is statistically significant, though this may be introduced in a future version of the software (Clarke and Warwick 2001). We used BIO-ENV to look for relationships between three pairs of datasets: the diatom community data vs. environmental variables; the live algae relative

Table II.1. List of the 52 most common benthic diatom species in the Bealey mire/tarn complex, with identification references. Identification (ID) categories: 1. indistinguishable from known species with a worldwide distribution; 2. known from Southern Hemisphere only; 3. close to a known species (minor differences); 4. unknown species in a known genus. Optima for pH, conductivity and gilvin calculated are calculated using weighted averaging. Optima are in bold for potential indicator species (see text).

Species	References	ID category	% (over all 20 samples)	No. of occurrences at Bealey	pH optima	Conductivity optima ($\mu S\ cm^{-1}$)	Gilvin (g_{440}) optima
Encyonema neogracile Krammer	Krammer 1997	1	10.9	13	6.3	9.5	2.7
Kobayasiella sp. 1		4	10.6	19	5.8	8.3	2.9
Brachysira wygaschii Lange-Bertalot	Lange-Bertalot & Moser 1994	1	9.9	15	**5.3**	7.1	3.6
Encyonopsis cf. *blanchensis* Krammer	Krammer 1997	3	6.1	13	**5.1**	7.6	4.6
Brachysira cf. *brebissonii* Ross (form 1)	Lange-Bertalot & Moser 1994	3	6.1	16	5.3	7.6	2.8
Brachysira cf. *brebissonii* Ross (form 2)	Lange-Bertalot & Moser 1994	3	5.7	13	6.0	8.0	2.7
Eunophora oberonica Vyverman, Sabbe & Mann	Vyverman et al. 1997	2	5.1	16	5.5	6.9	2.7
Frustulia rhomboides (Ehrenberg) De Toni	Krammer & Lange-Bertalot 1991-1997	1	4.5	20	5.7	8.7	2.8
Frustulia cf. *nana* Moser, Lange-Bertalot & Metzelin	Moser, Lange-Bertalot & Metzelin 1998	3	4.4	15	6.0	8.8	2.7
Frustulia magaliesmontana Cholnoky	Foged 1979	1	4.0	18	5.5	7.7	2.8
Eunotia bilunaris v. *mucophila* Lange-Bertalot & Norpel	Krammer & Lange-Bertalot 1991-1997	1	2.9	13	**5.4**	7.2	3.3
Neidium iridis (Ehrenberg) Cleve	Patrick & Reimer 1966	1	2.9	16	5.3	7.5	3.7
Tabellaria flocculosa (Roth) Kutzing	Krammer & Lange-Bertalot 1991-1997	1	2.5	13	6.5	15.5	2.4
Brachysira neoexilis Lange-Bertalot	Lange-Bertalot & Moser 1994	1	2.1	11	6.2	9.9	2.6
Kobayasiella cf. *madumensis* (Jorgensen) Lange-Bertalot	Lange-Bertalot 1996, 1999	3	1.5	9	5.3	7.7	4.1
Pinnularia subgibba Krammer	Krammer 1992	1	1.3	8	5.4	7.5	3.5
Pinnularia cf. *anglica* Krammer	Krammer 1992	3	1.3	17	5.5	7.9	3.3
Frustulia rhomboides var. *elongatissima* Manguin	Foged 1979	1	1.3	8	**6.5**	12.4	2.7
Fragilariforma virescens (Ehrenberg) Williams & Round	Williams & Round 1987	1	1.3	2	6.8	22.2	1.9
Eunotia cf. *rhomboidea* Hustedt	Krammer & Lange-Bertalot	3	1.2	15	5.4	7.9	3.5
Pinnularia cf. *oriunda* Krammer	Krammer 1992	3	1.2	16	6.2	9.9	2.8
Amphora bergrennii Cleve (= *Eunophora* sp. 1)	Cleve 1881, Vyverman et al. 1998	2	1.3	14	5.4	7.5	3.7
?*Chamaepinnularia* sp.	Lange-Bertalot & Metzelin 1996	4	1.0	12	5.5	8.5	3.0
Kobayasiella subtilissima (Cleve) Lange-Bertalot	Lange-Bertalot 1996, 1999	1	0.9	19	5.6	7.8	3.1
Frustulia rhomboides var. *saxonica* (Rabenhorst) De Toni	Krammer & Lange-Bertalot 1991-1997	1	0.9	11	6.0	7.8	2.9
Brachysira cf. *lehmanniae* Lange-Bertalot & Moser	Lange-Bertalot & Moser 1994	3	0.8	11	5.7	7.3	2.5

Stenopterobia delicatissima (Lewis) Van Heurck	Krammer & Lange-Bertalot 1991-1997	1	0.8	7	5.3	7.4	3.8
Stenopterobia denestriata (Hustedt) Krammer	Krammer & Lange-Bertalot 1991-1997	1	0.7	11	5.9	8.7	3.3
Rossithidium cf. *pusillum* (Grunow) Round & Bukhtiyarova	Krammer & Lange-Bertalot 1991-1997	3	0.6	12	6.0	8.5	2.8
Stenopterobia curvula (W. Smith) Krammer	Krammer & Lange-Bertalot 1991-1997	1	0.5	9	6.3	10.7	2.8
Brachysira styriaca (Grunow) Ross	Lange-Bertalot & Moser 1994	1	0.5	6	6.5	13.2	2.7
Eunotia incisa Gregory	Krammer & Lange-Bertalot 1991-1997	1	0.5	9	5.9	7.9	3.1
Brachysira cf. *brebissonii* Ross (form 3)	Lange-Bertalot & Moser 1994	3	0.4	11	6.1	10.7	2.6
Navicula gottlandica Grunow in Van Heurck	Krammer & Lange-Bertalot 191-1997, Vyverman, 1996	1	0.4	3	6.8	19.7	2.1
?Rossithidium sp. 1		4	0.4	4	6.8	19.7	2.1
Achnanthidium minutissimum (Kutzing) Czarnecki	Krammer & Lange-Bertalot 1991-1997	1	0.3	8	6.4	12.6	2.3
Nupela paludigena (Scherer) Lange-Bertalot	Lange-Bertalot & Moser 1994	1	0.2	3	5.3	6.5	3.0
Eunotia cf. *glacialis* Meister	Krammer & Lange-Bertalot 1991-1997	3	0.2	7	5.8	10.2	2.7
Achnanthes marginulata Grunow in Cleve & Grunow	Krammer & Lange-Bertalot 1991-1997	1	0.2	1	6.85	22.2	1.9
Eunotia praerupta Ehrenberg	Krammer & Lange-Bertalot 1991-1997	1	0.2	4	5.3	6.3	2.7
Encyonopsis cf. *aequalis* (W. Smith) Krammer	Krammer & Lange-Bertalot 1991-1997	3	0.2	3	5.5	7.3	2.8
Encyonopsis cf. *delicatissima* (Hustedt) Krammer	Krammer 1997	3	0.1	2	6.5	10.5	2.7
Adlafia sp.	Moser et al. 1998	4	0.1	3	5.2	6.7	3.0
Diadesmis sp.		4	0.1	3	6.7	17.3	2.4
Cymbella naviculiformis (Auerswald) Cleve	Krammer & Lange-Bertalot 1991-1997	1	0.1	1	6.85	22.2	1.9
Eunotia diodon Ehrenberg	Krammer & Lange-Bertalot 1991-1997	1	0.1	2	6.85	21.6	1.9
Encyonopsis sp. 1		4	0.1	1	6.85	22.2	1.9
Eunotia implicata Norpel, Lange-Bertalot & Alles	Krammer & Lange-Bertalot 1991-1997	1	0.1	6	5.5	6.6	2.3
Eunotia sp.		4	0.1	5	5.6	7.6	3.4
Navicula sp.		4	0.1	5	6.25	10.8	2.7
Pinnularia microstauron Ehrenberg (Cleve)	Krammer 1992	1	0.1	4	6.1	10.0	3.2
Encyonopsis sp. 2		4	0.1	2	6.0	8.8	3.1

abundance assessments vs. environmental variables and the diatom community data vs. live algae data (as environmental variables).

Because the above analysis confirmed strong environmental relationships with the diatom community, we used weighted averaging regression analysis (WA, Birks et al. 1990) to investigate the strength of models for predicting pH, conductivity and gilvin from the diatom community data, using C^2 software (Juggins 2003). The software calculates species optima and tolerances (respectively, the average and standard deviation of the environmental parameter over all sites where a taxon occurs, weighted by the relative abundance of the taxon at each site.) The predictive capability of the resulting models was assessed using the jackknife ("leave-one-out") cross-validation procedure. These techniques are standard for the construction of transfer functions for use in palaeolimnological studies (e.g. Hall and Smol 1992). In the present case, the procedure is relevant because it also enables a preliminary identification of taxa that may be suitable as indicators of particular conditions because of their narrow tolerance ranges. For this dataset criteria for potential indicator species are based on two of the criteria used by Fallu et al. (2000). Our criteria were 1) occurrence in at least 8 of the 20 sites, and 2) tolerance to the variable of interest < 0.75 x the mean tolerance for all the species. Untransformed species and environmental data were used for the WA analyses.

Results

Environmental characteristics

Pool size varied from approximately 6400 m^2 to about 8 m^2. The pool water was comparable in its chemistry with similar South Island water bodies sampled in the 2001 survey (Vanhoutte et al. in press). pH ranged from moderately acidic to almost neutral (pH 5.1 – 6.85), and in general declined across the wetland from west to east. Conductivity was very low (5.7 to 22.2 $\mu S\ cm^{-1}$). Gilvin ranged from g_{440} = 1.54 (optically clear water) to 5.25 (lightly brown-stained). A high proportion of the dissolved nitrogen in most pools was in organic form, with total dissolved nitrogen ranging from 178 to 607 $\mu g\ l^{-1}$, and the inorganic component (NH_4 + NO_3) ranging from 10.8 to 61.2 $\mu g\ l^{-1}$. Of the cations measured, Na predominated in most sites (though at low levels, range 0.31–1.01 mg l^{-1}), consistent with the expected largely ombrotrophic hydrological regime. Ca was very low at most sites, but was noticeably higher at sites 13 and 14 (which were connected to a stream) and in pools 15 and 19, suggesting that the latter two sites also received some stream inputs (range over all sites 0.14–3.21 mg l^{-1}). Data for all the sites are summarized in Table II.2.

Community composition

In the inverted microscope assessments, diatoms were assigned a score of 5 or more at 18 of the 20 sites (Table II.3), with the lowest score (3) at site 1. Diatoms dominated at sites 8, 9 and 12. Detritus (mainly decaying sphagnum and other vegetation) was dominant in all other samples

Table II.2. Physical and chemical variables measured in 20 pool sites in the Bealey wetland area, September 2001.

	Approx. area (m^2)	Depth (cm)	temp. (°C)	pH	Conductivity ($\mu S\ cm^{-1}$)	Gilvin g_{440}	DRP ($\mu g\ l^{-1}$)	NH_4 ($\mu g\ l^{-1}$)	NO_3 ($mg\ l^{-1}$)	TDP ($\mu g\ l^{-1}$)	TDN ($\mu g\ l^{-1}$)	DOC ($mg\ l^{-1}$)	Ca ($mg\ l^{-1}$)	Mg ($mg\ l^{-1}$)	Na ($mg\ l^{-1}$)	K ($mg\ l^{-1}$)	Cl ($mg\ l^{-1}$)	SO_4 ($mg\ l^{-1}$)	SiO_2 ($mg\ l^{-1}$)
1	16	40	7.4	5.22	6.21	2.86	1.5	24.0	5.0	3.1	282	6.3	0.34	0.07	0.46	0.19	3.6	0.1	0.57
2	150	40	6.4	5.47	6.96	2.19	1.5	14.0	1.9	2.8	326	3.7	0.27	0.08	0.68	0.10	3.9	0.1	0.34
3	75	37	6.4	5.13	6.57	3.98	0.9	11.2	2.0	1.7	296	8.4	0.30	0.07	0.44	0.12	3.3	0.1	0.43
4	30	33	4.9	5.08	8.7	4.91	1.1	16.4	2.6	2.4	444	9.2	0.54	0.11	0.68	0.34	3.6	5.6	0.32
5	40	33	4.9	5.08	7.39	5.25	1.0	10.3	2.3	1.9	296	10.3	0.47	0.09	0.54	0.25	3.4	0.1	0.45
6	64	28	6.7	5.1	7.15	4.81	1.5	13.8	2.8	2.2	326	10.8	0.40	0.08	0.44	0.21	6.6	0.1	0.55
7	300	38	7.2	5.1	6.44	3.20	1.5	16.3	2.7	2.2	341	7.2	0.14	0.06	0.40	0.07	3.4	0.1	0.56
8	6400	33	7.1	5.6	6.82	2.92	0.6	16.5	3.4	2.4	311	6.3	0.52	0.08	0.73	0.20	3.5	0.1	0.44
9	6400	33	7.8	6.25	7.86	3.16	4.0	36.8	4.3	5.9	607	5.5	0.58	0.10	0.85	0.22	3.6	0.1	0.50
10	40	19	7.7	6.15	9.06	2.90	4.3	56.1	5.1	6.0	592	6.2	0.68	0.10	0.97	0.26	6.7	0.1	0.28
11	10	35	7.2	5.83	8.37	3.20	6.0	48.8	5.2	7.5	726	7.3	0.51	0.08	0.98	0.20	3.7	0.1	0.62
12	1600	32	9.3	6.2	5.72	1.54	1.2	12.1	2.6	2.9	267	3.9	0.41	0.06	0.40	0.18	3.5	0.1	0.50
13	8	30	3.8	6.85	22.21	1.89	1.5	18.0	3.9	3.1	281	6.2	3.21	0.17	0.98	0.21	3.8	6.3	0.77
14	10	24	2.5	6.55	12.34	2.95	1.1	13.4	15.0	2.5	222	6.9	1.44	0.09	1.01	0.30	3.9	5.7	0.53
15	500	20	6.8	6.55	11.76	2.56	2.0	23.6	6.2	3.5	326	4.6	1.04	0.07	0.66	0.23	3.6	5.5	0.38
16	200	41	1.2	5.25	6.66	2.12	0.5	10.4	1.7	1.5	178	3.6	0.39	0.06	0.54	0.29	3.8	0.10	0.53
17	200	25	8.2	5.37	7.92	2.44	1.7	24.5	4.1	3.3	355	6.0	0.44	0.07	0.62	0.31	4.0	8.0	0.49
18	140	30	8.2	5.37	7.77	2.46	1.0	8.8	2.0	3.0	267	7.8	0.39	0.07	0.55	0.32	4.0	0.1	0.60
19	3300	26	6.5	6.43	10.23	2.69	1.3	11.9	1.8	2.9	267	8.5	1.16	0.08	0.66	0.16	3.6	0.1	0.80
20	75	40	7.4	6.5	10.6	2.74	1.5	14.8	2.5	2.9	260	5.6	0.41	0.03	0.31	0.15	12.9	0.1	0.26
	Mean	31.85	6.38	5.75	8.84	3.04	1.79	20.09	3.86	3.21	348	6.72	0.68	0.08	0.64	0.22	4.42	1.63	0.50
	Std. Dev.	6.62	2.00	0.61	3.65	1.00	1.38	12.91	2.93	1.54	139	2.05	0.67	0.03	0.22	0.07	2.21	2.76	0.14

Table II.3. Relative abundance of main substrate constituents in raw samples from 20 pools at Bealey Spur. The relative abundance scale used ranges from 8 (dominant) to 1 (rare).

Site	Relative abundance of main constituents							
	Cyanobacteria			Diatoms	Desmids	Green algae	Organic detritus	Inorganic
	Fine trichomes	Coarse trichomes	Colonial unicells					
1	1	1	2	3	4	3	8	3
2	8	1	5	5	1	0	6	0
3	2	1	7	6	1	2	8	1
4	3	2	4	6	2	1	8	3
5	2	1	0	7	1	1	8	4
6	1	0	4	7	3	2	8	1
7	3	3	4	7	2	1	7	8
8	7	2	6	8	5	1	6	2
9	2	2	3	8	5	2	6	1
10	4	0	3	4	2	1	8	3
11	4	1	3	6	3	2	8	2
12	7	1	4	8	4	2	3	2
13	0	0	0	6	2	1	8	1
14	0	0	0	6	5	1	8	3
15	2	2	3	6	5	3	8	0
16	1	0	1	5	3	0	8	2
17	2	0	3	5	1	2	8	3
18	5	0	3	5	3	0	8	3
19	8	2	3	7	6	5	4	2
20	4	0	2	7	2	2	8	1

except sites 2 and 19 where the main constituent was fine cyanobacterial trichomes (*Leptolyngbya* sp.). Green algae other than desmids were uncommon, though a species of *Oedogonium* was recorded at 17 sites.

Eleven genera made up 95% of the diatom community overall. These were (in order of abundance): *Brachysira*, *Frustulia*, *Kobayasiella*, *Encyonema*, *Encyonopsis*, *Eunophora*, *Eunotia*, *Pinnularia*, *Neidium, Tabellaria* and *Stenopterobia*. Eighty-one diatom morphospecies in 31 genera were distinguished. Total species richness at individual sites ranged from 18 (site 12) to 40 (site 13). Fifty-two common species (with an abundance over all 20 sites of >0.1%) are listed in Table II.1 along with calculated optima for pH, conductivity and gilvin, and the identification category (see Methods). Of these, 27 were indistinguishable from known cosmopolitan taxa (category 1) and two (*Eunophora* spp.) were known only from the Southern Hemisphere. The remaining taxa were problematic in that they did not correspond exactly to any species in the available literature. Some of these indeterminate species were very common and had distinctive distinguishing features. A complete taxonomic treatment of the species found will be presented elsewhere (see paper VI).

The seven most common diatom species: *Encyonema neogracile*, *Kobayasiella* sp. 1, *Brachysira wygaschii*, *Encyonopsis* cf. *blanchensis*, two forms of *Brachysira* cf. *brebissonii*, and *Eunophora oberonica*, accounted for large proportions of the community at most sites (typically >50%), but there were marked shifts in composition across the wetland. For example, *E.* cf. *blanchensis* occurred in high relative abundances only at sites with low pH, while *Encyonema neogracile* tended to occur in the pools with higher pH. At site 13, a pool in a stream, these seven taxa comprised only 6.5% of the community, which was dominated by *Fragilariforma virescens* and *Tabellaria flocculosa*. Two species of *Eunophora* were recorded over the whole wetland: *Eunophora* sp. 1 (Vyverman et al. 1998, see below) (at 14 sites) and *E. oberonica* (at 16 sites). The latter species was abundant, comprising >13% of the community at four sites.

Note that although site 13 differed from the other sites in its much higher conductivity and lower relative abundances of the common diatom taxa, we consider that the site lies at one end of a natural continuum in the Bealey wetland, from isolated water bodies to flowing water. Therefore the site was retained in the community – environment analyses. To check the influence of this site, BIO-ENV analyses were also run omitting site 13.

Diatom community – environment relationships

The BIO-ENV analysis on all data produced a best rank correlation between the diatom and environmental matrices of $\rho_s = 0.763$ for a combination of pH and conductivity. Addition of gilvin caused the match to deteriorate very slightly ($\rho_s = 0.757$). pH only yielded $\rho_s = 0.739$, conductivity only, $\rho_s = 0.548$ and gilvin only, $\rho_s = 0.293$. A comparison of MDS plots derived from the diatom dataset and from pH + conductivity shows good visual correspondence (Figure II.2). Addition of gilvin (Figure II.2c) increases the distance between sites 11 and 12, which corresponds to the biotic MDS, as does increased separation of sites 4, 5 and 6 from sites 3, 7 and 16. However, to offset this, site 1 is positioned much farther from the biologically similar 4, 5 and 6 (Figure II.2a). The best result with site 13 omitted was $\rho_s = 0.738$ for pH only, followed by $\rho_s = 0.685$ for a combination of pH, conductivity and gilvin.

Histograms of the abundance of common species vs. sites arranged in order of pH show that several taxa were strongly influencing the separation of communities (Figure II.3). In particular, *Encyonema neogracile*, *Encyonopsis* cf. *blanchensis*, *Brachysira neoexilis*, and *Neidium iridis* showed marked clustering.

Both BIO-ENV analyses involving the relative abundance assessment data on the whole algal community (with and without site 13) gave low maximum values for rank correlation ($\rho_s < 0.355$).

Weighted averaging regression and calibration produced a strong model for predicting pH. The best result used simple WA regression (no tolerance down-weighting) with classical deshrinking (Birks et al., 1990). Jackknife-derived predicted pH values matched the measured values well (Figure II.4, $R^2 = 0.91$, RMSEP = 0.18). The residuals plotted against predicted values (Racca and

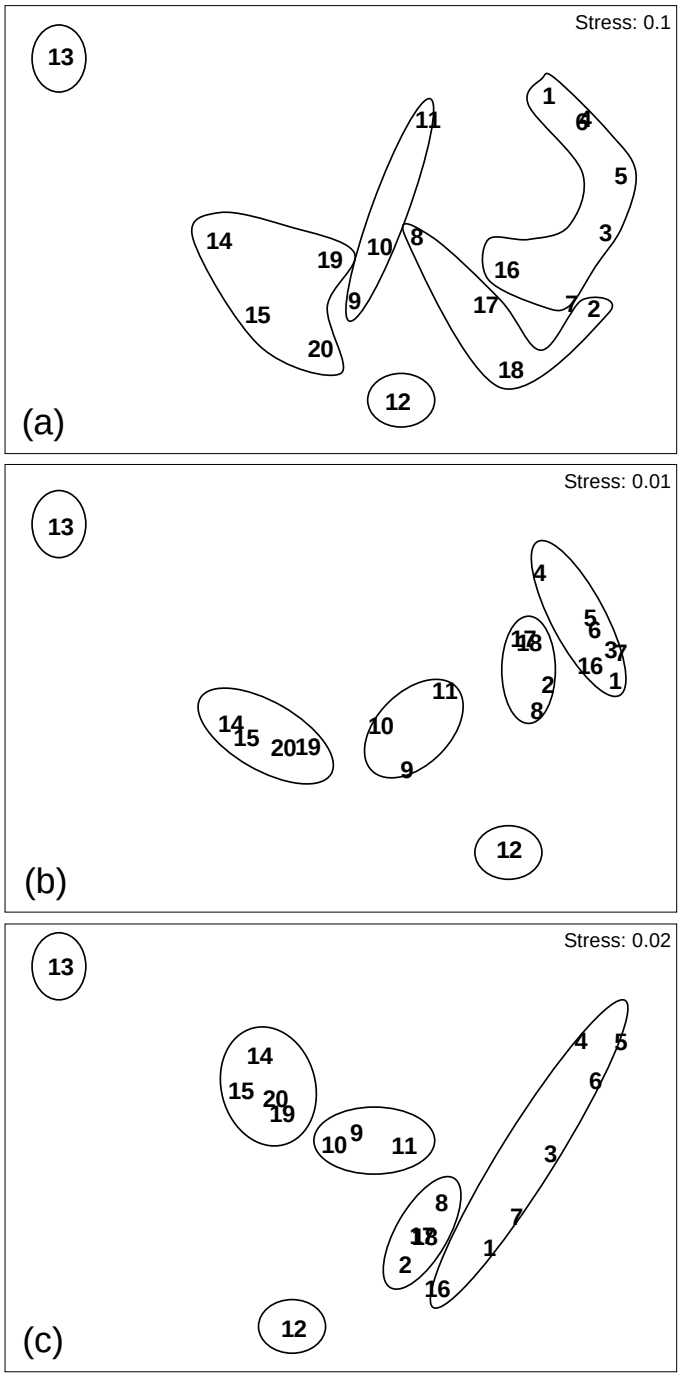


Figure II.2. Non-metric multidimensional scaling (MDS) plots for (a) square-root transformed diatom community data, (b) pH and conductivity, (c) pH, conductivity and gilvin. The circled groups on the best-fitting abiotic plot (b) indicate sites that have similar pH and conductivity. The same sites are grouped on the biotic plot (a) to highlight the relatively good visual match between the two plots. In (c) the right-hand group of 7 sites are separated along a gradient of gilvin. This appears to improve the match with (a), except for the position of site 1 (see text). A stress value of 0.1 for the biotic MDS indicates a good representation of the 20 sites in two dimensions. Stress values for the abiotic plots are low because a maximum of 3 variables was used to construct the plots.

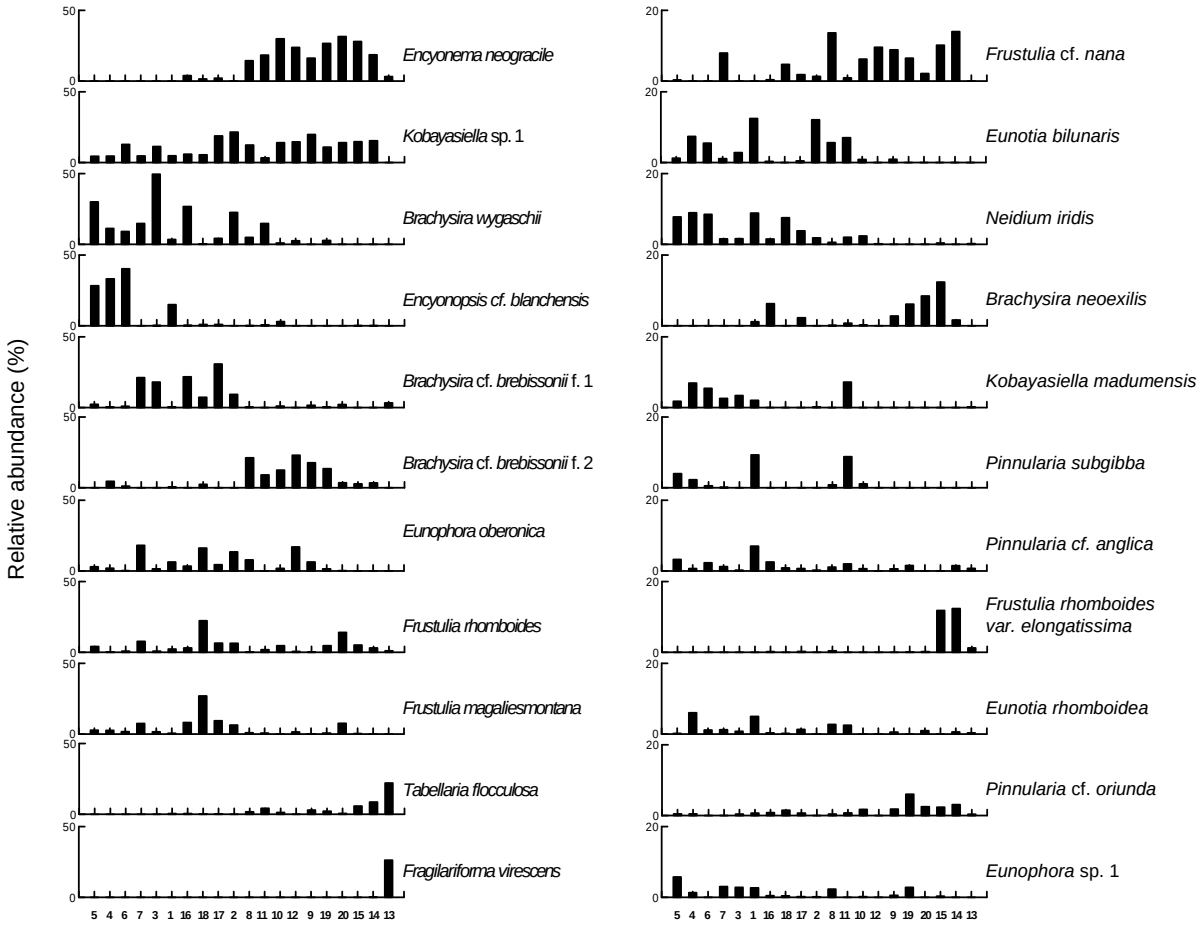


Figure II.3. Relative abundances at each site of the 22 most common diatom taxa plotted with sites arranged in order of increasing pH. Note the different vertical scales in the two columns.

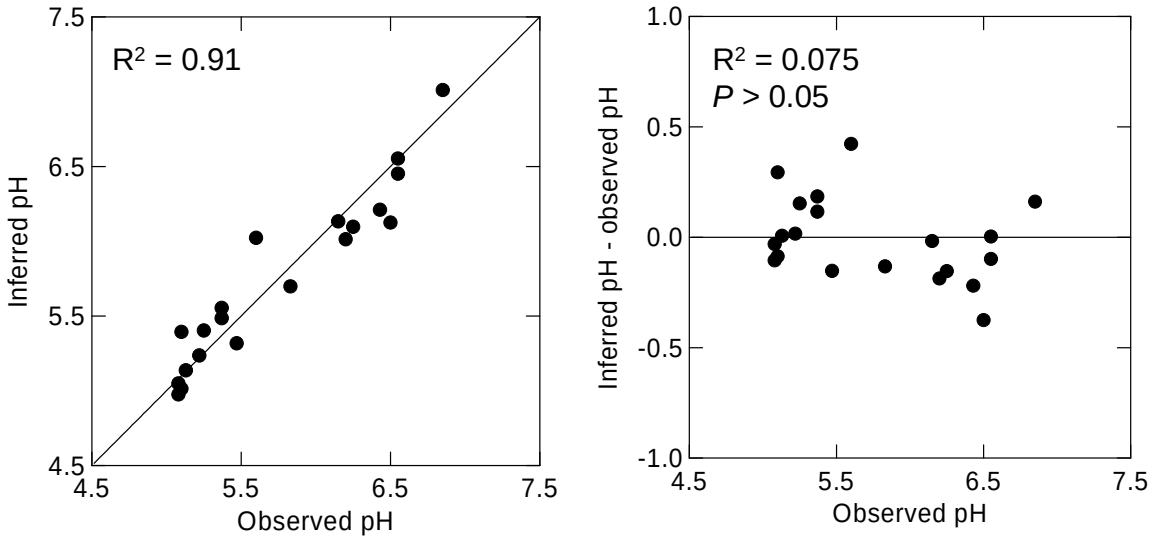


Figure II.4. Observed pH values at the 20 pool sites plotted against predicted values calculated from a WA model (see text). The right-hand graph shows that there is no bias in the residuals.

Prairie 2004) indicated no bias in the model (Figure II.4). A similar model for predicting conductivity produced predicted values that correlated well with the measured values ($R^2 = 0.88$, RMSEP = 1.55, data not shown) but there was considerable bias in the predictions as a result of the high conductivity at site 13. A model for gilvin performed poorly (data not shown).

Four diatom taxa met the criteria specified for potential use as indicator species for pH: *Encyonosis* cf. *blanchensis* (pH 5.1), *Brachysira wygaschii* (5.3), *Eunotia bilunaris* var. *mucophila* (5.4) and *Frustulia rhomboides* var. *elongatissima* (6.5).

Neither species of *Eunophora* showed up as a potentially good indicator of pH. Separate BIO-ENV analyses run for the two species showed no strong correlation with any of the environmental variables measured (either singly or in combination). For example, the best correlation for *E. oberonica* (untransformed data) was $\rho_s = 0.540$ (a combination of conductivity, NO_3, Na and Cl).

Discussion

The diatom communities found in the Bealey Spur pools are generally consistent at the genus level with the characteristic "peat-bog flora" found in other regions and dominated by species of *Eunotia*, *Pinnularia*, *Frustulia* and *Brachysira*. This flora appears to have a global distribution (Scherer 1988 and references therein). For example, Gaiser and Johansen (2000) studied the diatom communities in South Carolina lowland wetlands and reported similar assemblages, which also included *Neidium*, *Kobayasiella*, *Stenopterobia*, *Encyonema* and *Encyonopsis*. Studies in Tierra del Fuego (Mataloni 1999) and Japan (Watanabe et al. 2000) have yielded the same genera and species. The taxa found evidently reflect an association with the dystrophic, low-nutrient, acidic conditions typical of mire-pool environments, and this association appears to be independent of latitude and altitude (temperature) (Scherer 1988). However, as Vyverman et al. (1995) found in Tasmania, there did seem to be a distinctive regional element in this New Zealand dataset.

The occurrence of two species of *Eunophora* at Bealey represents a major difference between this New Zealand peat-bog flora and those reported from elsewhere. *Eunophora* was first found as a common component of the diatom flora in oligotrophic and dystrophic lakes in the Tasmanian highlands (Vyverman et al. 1995). The genus currently includes three species (*E. oberonica*, *E. tasmanica* and *E. indistincta*) plus a fourth species (*Eunophora* sp. 1) previously described as *Amphora berggrenii* Cleve, which, prior to the Tasmanian survey had been known only from fossil material in New Zealand (Vyverman et al. 1998). Although *Eunophora* was widespread in Tasmania and common in some samples, Vyverman et al. (1998) reported that they had "never found thriving populations of *E. oberonica*…", though live cells of *Eunophora* sp. 1 were "a little more abundant". In the 2001 survey in South Island, New Zealand, *Eunophora* occurred at >50% of the sites sampled, mainly in alpine pools and tarns with organic sediments and water with pH < 6 (K. Vanhoutte, pers. comm.). Relative abundances of up to 11% were recorded for *E. oberonica* (Edwards Valley, Arthurs Pass) and up to 2.5% for *Eunophora* sp. 1 (Staircase Saddle, Fiordland)

and both these samples contained many live specimens. In the present study at Bealey Spur, examination of preserved material showed high relative abundances of live cells of both *E. oberonica* (up to ~15%) and *Eunophora* sp. 1 (up to >5.5%) at several sites.

In Figure II.5 we plot the relative abundances of both species in sites grouped by the pH classes used to examine the Tasmanian populations (Vyverman et al. 1998). This shows that at Bealey, the pH preferences of the two species cover a broad range, but differ. However, the optimal pH ranges found in Tasmania and Bealey are different again. Vyverman et al. (1998) found *Eunophora oberonica* in highest abundance in their most acidic sites (pH < 4.8, not represented in the present survey), whereas at Bealey the highest abundances were at pH 5.2 – 6.4. Conversely *Eunophora* sp. 1 had highest abundance in lower pH environments at Bealey (pH < 5.2) compared to pH > 6 in Tasmania. Thus, although *Eunophora* is generally restricted to dystrophic, acidic to slightly acidic, low nutrient waters, in cool areas (mainly high altitude) its distribution within these environments appears to be driven by factors other than water chemistry.

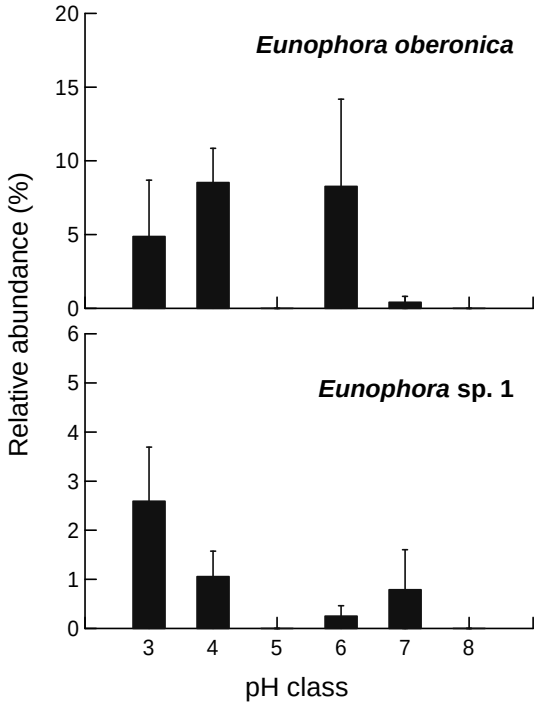


Figure II.5

Mean relative abundance (%, with standard error bars) of *Eunophora oberonica* and *Eunophora* sp. 1 occurring at Bealey in the pH classes used by Vyverman et al. (1998). pH classes are: **3**, 4.81–5.2; **4**, 5.21–5.6; **5**, 5.61–6.0; **6**, 6.01–6.4; **7**, 6.41–6.8; **8**, 6.81–7.2. Classes 1 and 2 (pH 4.0–4.8) did not occur at Bealey. Classes 5 and 8 were represented by only one site each at Bealey.

In ongoing investigations at Bealey Spur, we have observed that thriving populations of live *E. oberonica* tend to occur in pools where the substrate is consolidated into a firm cyanobacterial mat, though this is not always the case. The cyanobacterial mats resemble those found in Antarctic freshwater systems (Sabbe et al. 2004) and comprise a mixture of fine trichomes (*Leptolyngbya* sp.), closely packed colonial unicells, and larger taxa including *Dichothrix*, *Stigonema* and *Scytonema*. They are organised into a yellow-brown pigmented layer overlying a bright green zone, where most of the live diatom cells are located. At Bealey, such mats were best developed at sites

8, 9 and 12, all of which had relatively high concentrations of *E. oberonica*. Other diatoms common at these sites (generally >15% relative abundance) included *Encyonema neogracile*, *Kobayasiella* sp. 1, and *Brachysira* cf. *brebissonii* form 2. Given that cultures of *E. oberonica* have shown extremely slow rates of cell division (one division every 2-3 weeks, V. Chepurnov, pers comm.) it is possible that very stable physical conditions may be required for the development of large populations. The cyanobacterial mats may provide suitably stable conditions. Work is underway to investigate this possibility and is reported in part in paper IV.

To date, *Eunophora* species have been reported only from Tasmania and New Zealand (Vyverman et al. 1998, K. Sabbe, pers. comm.). Thus, the occurrence of *Eunophora* species in New Zealand as a major component of the otherwise globally distributed "peat-bog flora" (at the genus level) raises some interesting questions. Is *Eunophora* confined to New Zealand and Tasmania because these are the only locations where suitable conditions exist for populations to thrive? Has the geographic isolation of suitable habitats in New Zealand and Tasmania, combined with slow growth rates, ensured that the genus has retained a restricted distribution? Does *Eunophora* form part of a regionally distinctive high-altitude diatom flora that has been less subject to invasions by cosmopolitan taxa than communities at low-altitude locations populated by humans? Given that many cosmopolitan species also appear to be thriving at the sites sampled in the present study, what are the specific conditions that allow *Eunophora* species to do well in the same environment? A complicating factor is that the pH data discussed above suggest not only that *E. oberonica* and *E.* sp. 1 have different environmental preferences, but that these vary with location. Studies on live populations of both species, and the cosmopolitan taxa associated with them, are probably the only way to begin answering the last of these questions.

With regard to the diatom communities as a whole, although the sensitivity of diatom community composition to pH has long been known and is well documented (see Battarbee et al. 1999 for a review), this is the first time such a strong relationship between diatom community composition and pH has been demonstrated in New Zealand. The South Island-wide survey of 71 sites in 2001 also showed pH (and related variables) to be the main environmental factor influencing diatom community composition, though that analysis was based on genus level data (K. Vanhoutte, pers. comm.). Reducing our dataset to genus level and re-running the BIO-ENV procedure resulted in a correlation coefficient of $\rho_s = 0.682$ for a combination of pH, conductivity and gilvin. This confirms the result found with the species data, but demonstrates it less convincingly.

Diatom assemblages have been used to produce robust models for predicting alkalinity, conductivity and DOC in other studies (Fallu et al. 2000, Davies et al. 2002, Fritz et al. 1999). In this study, there appeared to be a response to conductivity along a very small range (5.7 – 22 μS cm^{-1}). Conductivity was strongly correlated to Ca, which is in turn correlated with alkalinity at several sites at Bealey (Kilroy et al. in revision [III]). Therefore this result is also consistent with

findings elsewhere. However, the conductivity – diatom community relationship was strongly influenced by site 13, where conductivity was almost twice as high as the next highest value. The BIO-ENV procedure run omitting site 13 confirmed that pH was by far the most important variable influencing diatom communities at the remaining 19 sites.

The relatively poor model for gilvin is to be expected given the confounding effect of a very strong pH gradient over a small number of sites. Nevertheless, there is evidence for a link between gilvin and community composition at Bealey. Figure II.3 shows that deterioration of the diatom community–environment match by addition of gilvin is largely due to inconsistency in the positioning of site 1. (Compare the relative positions of sites 1 and 4, 5, 6 in Figures II.2a, b, c, and note the increased separation in c). This pool was observed to have dried out later in the summer. A tendency to desiccate probably explained the low relative abundance of live diatoms at site 1 (Table II.3), but may also have influenced the water chemistry–diatom community relationship. Indeed, re-running BIO-ENV omitting site 1 produced an optimum correlation coefficient of ρ_s = 0.799 for a combination of pH, conductivity and gilvin.

These discrepancies highlight the fact that a larger dataset would be more likely to yield robust models, a point also made following other studies involving relatively small datasets (Peinitz and Smol 1993, 22 lakes; Battarbee et al. 1997, 24 lakes and streams). Thus it would be desirable to expand the present dataset with information from different locations.

There is increasing interest in the use of diatom communities for inferring past environmental conditions in New Zealand although to date most emphasis has been placed on salinity gradients (Goff et al. 2000, Cochran, 2002). However, the first transfer function for inferring trophic status (as chlorophyll *a*), conductivity and pH in medium to large New Zealand lakes is now completed (Reid 2005). The present study represents an early step towards extending the potential range of palaeoecological studies into alpine and treeline zones. Interpretation of inferred pH, conductivity and gilvin from cores taken from subalpine mire pools is likely to be difficult, given the complex way in which mires develop over time and interact with climate (Foster and Wright 1990). Multiple proxies to provide independent chronologies will almost certainly be necessary. For example, a chironomid-based transfer function for temperature is currently under development (M. Reid, pers. comm.). In the meantime, the results from this relatively small survey also indicate that regional identification guides are needed in order to capitalise on the environmental indicator capacity of high-altitude diatom communities in New Zealand.

2.III Spatial and temporal variability in mire pool limnology

Introduction

Mires (peat-accumulating wetlands) are increasingly being studied because of early impacts from global climate changes (Bragg and Tallis 2001, Pastor et al. 2003), their potential contribution to climate change (Mäkilä et al. 2001, Bragg 2002), and their ecological diversity (Gunnarsson et al. 2000, Watanabe et al. 2000, Lederer and Soukupova 2002). Mires formed following glaciation in areas of poor drainage, cool temperatures and consistent rainfall, which allowed the accumulation of partly decomposed vegetation and development of dystrophic open-water pools (Foster and Fritz 1987). Such wetlands are widespread in the Northern Hemisphere, but less so in the south (Mark et al. 1995). Nevertheless, the glaciated terrain of subalpine regions in New Zealand contains numerous terraces and depressions in which mires have developed, with associated pools and tarns. Examples have been studied from the perspective of vegetation and vegetation history (e.g., Agnew et al. 1993, Mark et al. 1995, McQueen and Wilson 2000, Walker et al. 2001), palaeoecology (McGlone et al. 1995), water balance (Campbell and Williamson 1997), and peat/water chemistry and vegetation (Dickinson et al. 2002).

Recently, tarns (predominantly mire pools) and bogs in New Zealand were shown to contain higher proportions of endemic benthic diatoms than other freshwater habitats (Kilroy et al. 2007 [I]). This was attributed to low levels of disturbance and low productivity in these systems at the landscape scale. However, information is lacking on environmental characteristics of these systems at scales relevant to aquatic microorganisms (i.e., within individual mire pools and across seasons). Further, it is not known whether Southern Hemisphere mires conform to the same gradients as equivalent Northern Hemisphere environments.

It is well established that variability in water chemistry between open-water bodies in the same mire system is linked to water source (ombrotrophic versus minerotrophic) and degree of water movement (Sparling 1966), and to the age and size of pools (Foster and Fritz 1987). Thus, pools in a mire might be expected to span a wide range of chemical conditions leading to potential differences in aquatic communities. Temporal investigations on mires to date have generally focussed on the vegetative or ice-free seasons (e.g., Bragazza 1994, Vitt et al. 1994, Tahvanainen et al. 2003), although there have been longer studies in more temperate areas (Proctor 2006). Yet water-chemistry consequences of physical seasonal changes (temperature, light) may directly impact on benthic and planktonic aquatic biota. For example, winter reductions in pH (Arvola et al. 1990) might be significant for pH-sensitive species. Although ombrotrophic areas (bogs) are by definition nutrient deficient, receiving only atmospheric inputs, increased microbial activity in summer could enhance turnover and release of nutrients (N and P) from the organic substrate in

pools, potentially leading to enriched aquatic conditions in temperatures favourable for algal growth.

In the present study, on a representative mire in South Island, New Zealand, we explored pool-water environments in four contrasting pools over two full seasonal cycles. Our primary aim was to characterise the spatial and temporal variability of a range of physical, chemical and productivity variables, including an assessment of the temporal coherence of variables among pools. We discuss the chemical characteristics of these pools compared with those of mire pools elsewhere, and other freshwater systems.

Methods

Study area

The investigation took place at Bealey Spur wetland (approximately 1000 m a.s.l.) adjacent to Arthur's Pass National Park, South Island, New Zealand (Figure III.1). The 7-ha mire declines in elevation from west to east by approximately 10 m and comprises a complex of pools on peat base. Vegetation is predominantly *Empodisma minus*, interspersed with tussock (*Chionochloa* sp.), a low-growing *Dracophyllum* species, and *Sphagnum* sp.. Herbs such as *Drosera* sp. are frequent in the wetter areas. For further details of the study area, refer to Kilroy et al. (2006 [II]). Four pools in the wetland were selected on the basis of a gradient in water colour using data from an earlier synoptic survey (Kilroy et al. 2006 [II]). The four pools differed in size, but had similar depths at the sampling locations (mean 28 cm, s.d. 1.4 cm), and all had a substrate of deep (>1 m), soft organic material, typical of mire pools (Foster and Fritz 1987). Pool A was the smallest at approximately 40 m^2. Pool B was the largest open water body in the wetland (approx. 4400 m^2), ca. 100 m from pool A and at a similar elevation. Pool C was a moderate sized pool (700 m^2), which was elevated 3-4 m above pools A and B, and flanked by numerous smaller pools on the same level. Pool D (1100 m^2) was at the highest but narrowest area of the wetland, close to the base of hillslopes to the north and south, and again flanked by pools of variable size.

Sample collection and processing

At the beginning of the study period, an automatic rain gauge was installed near the centre of the wetland area and staff gauges were installed at each of the four pool sites (Figure III.1). Water temperature was logged at 15 minute intervals in each pool (Hobo loggers, Onset Computer Corporation). From February 2002 to April 2004, the wetland was visited at approximately 2-weekly intervals (mean 14.1 ± 2.9 days). On each visit, we recorded water level, depth, pH and conductivity in each pool. Water samples were collected from just above the substrate approximately 0.6 m from the pool edges for subsequent analysis for nutrients (dissolved reactive phosphorus, NO_3, NH_4, and total dissolved N and P), dissolved organic carbon (DOC), water colour (absorption coefficient at 440 nm, g440), and alkalinity. Material filtered from up to 1 litre of water was analysed for chlorophyll *a* and particulate N and P (for subsequent calculation of total

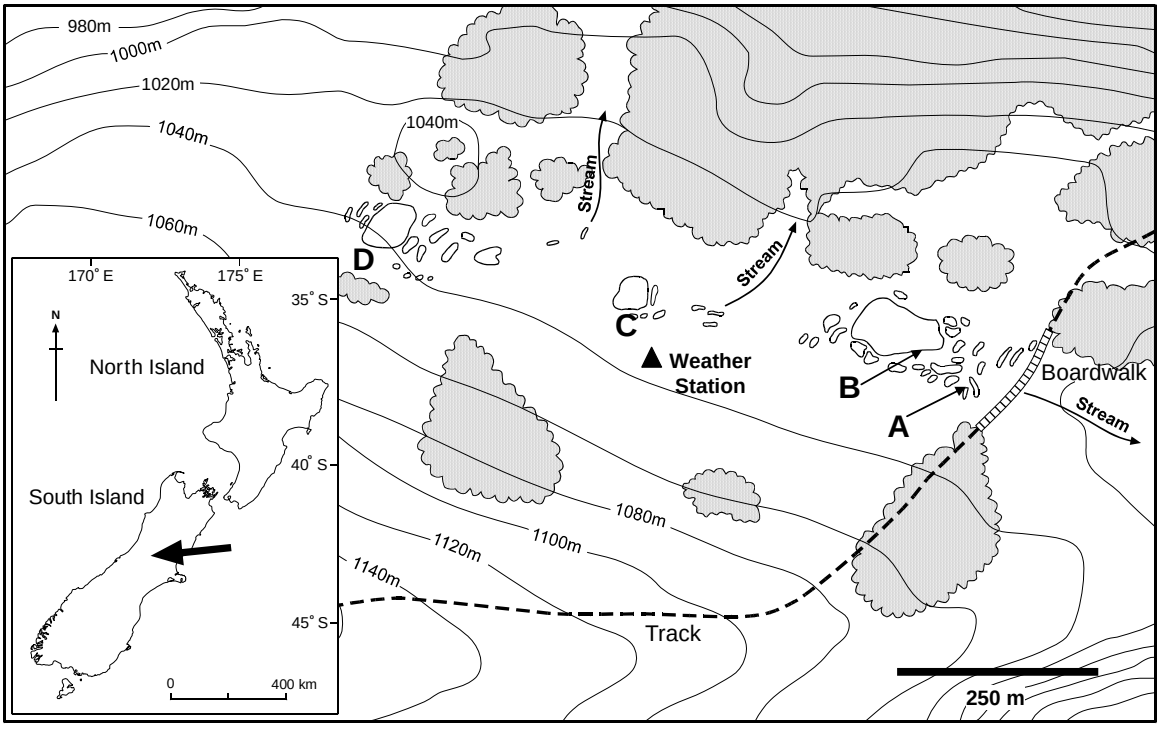


Figure III.1. Location map of the study area and sampling sites (A to D). The shaded areas represent beech forest (*Nothofagus* sp.).

N and P). Alkalinity was determined by end-point titration. Chlorophyll *a* was extracted in cold acetone (after grinding), then fluorescence at 431 and 670 nm was read fluorometrically (with correction for phaeophytins) (Downes 1988). On every fourth visit, we collected additional water samples for analyses of major ions. Water column nutrients and major ions were analysed as outlined in Kilroy et al. (2006 [II]). In the period of winter ice cover, sampling was undertaken so as to minimise disruption to the ice sheet, including replacement of removed ice cores following sampling whenever this was practicable.

Data analysis

Rainfall was incorporated into the main data set as total rainfall over one and 15 days prior to each sampling occasion. Water temperatures were averaged over 24 h and 10 days and the 10-day means were used to define seasons with summer >12 ºC and winter <5 ºC. We estimated the anion deficit (e.g., as in Tahvanainen et al. 2002) as the sum of major cations (H^+, NH_4^+, Ca^{2+}, Mg^{2+}, Na^+, K^+) minus the sum of major anions (Cl^-, SO_4^{2-}, HCO_3^- [from alkalinity]) in μEq l^{-1}. Time series of all variables (Table III.1) were log (*n*+1)-transformed, as necessary. We generated Pearson correlation matrices for the entire dataset across all four pools, and then for each pool individually. Significance values were Bonferroni-corrected. Time-series plots of selected variables provided visual representations of spatiotemporal variability. Coefficients of variation (%CV) summarised

temporal variability when calculated within pools and spatial variability when calculated across all pools. Overall and between-pool differences were also summarised using one-way ANOSIM (Primer v. 5), on the 12 variables in Table III.1c, nutrient (N and P) variables, and major ion data only (Table III.1e). We used ANOVAs to identify significant differences among means of individual variables across pools.

Temporal coherence was assessed by generating correlation matrices for all 21 variables listed in Table III.1 for each pair of pools, then calculating mean coherence (Pearson correlation coefficient, *r*) across all variables for each pair, and across all pairs for each variable (Magnuson et al. 1990). We used data from all available sampling occasions ($n = 15$ (dissolved ions), or $n = 51 – 57$ (other variables)). The proportion of strong correlations (Bonferroni-corrected $P < 0.05$) was also determined for each pool pair and each variable. We assigned each variable to a group based on its source or function, viz. physical variables, ions derived mainly from groundwater or rainfall, water properties resulting from contact with soil/vegetation, biologically important nutrients, and direct biological measurements (Table III.1). We then calculated mean coherences for each group.

All analyses other than ANOSIM were carried out using SYSTAT v. 11.

Results

Physical conditions

Mean water temperature over the entire sampling period and in all pools was 10.1 °C, with daily means in the warmest and coldest months of 17.6 °C (January) and 3.4 °C (June). Water temperature exceeded 30 °C on at least one occasion in all four pools in 2002/3, but reached only 25 °C in 2003/4. The detailed temperature record indicated diurnal fluctuations of up to 15 °C in summer (not illustrated). Summer – winter temperature differences were lowest in Pool A (Figure III.2a), though the overall temperature differences were not significant (data not shown). All pools were ice-covered for at least two months in winter (June and July) to a maximum thickness of 140 mm at the sampling sites. Annual rainfall over the sampling period was approximately 1800 mm, with no clear seasonal pattern over the two years of the study (Figure III.2b). Water level fluctuations were consistent across the four pools, but were muted in pools B and D compared to A and C (Table III.1, Figure III.2c).

Correlations across and within pools

Correlation analyses run on the complete 2-year dataset showed many significant relationships. In all pools, TN and TP strongly covaried with TDN and TDP, respectively, therefore the latter only were included in ANOSIM and temporal coherence analyses. With data from all four pools combined, water temperature, pH, conductivity, and chlorophyll *a* were significantly inter-related ($r = 0.320 – 0.753$, $P < 0.001$). Further intercorrelated sets were: pH, conductivity, alkalinity, Ca and Mg ($r = 0.478 – 0.827$, $P < 0.05$); pH, alkalinity and water colour (inversely) ($r = -0.340 – 0.793$, $P < 0.05$); water level and rainfall variables ($r = 0.337 – 0.527$, $P < 0.001$); chlorophyll *a*,

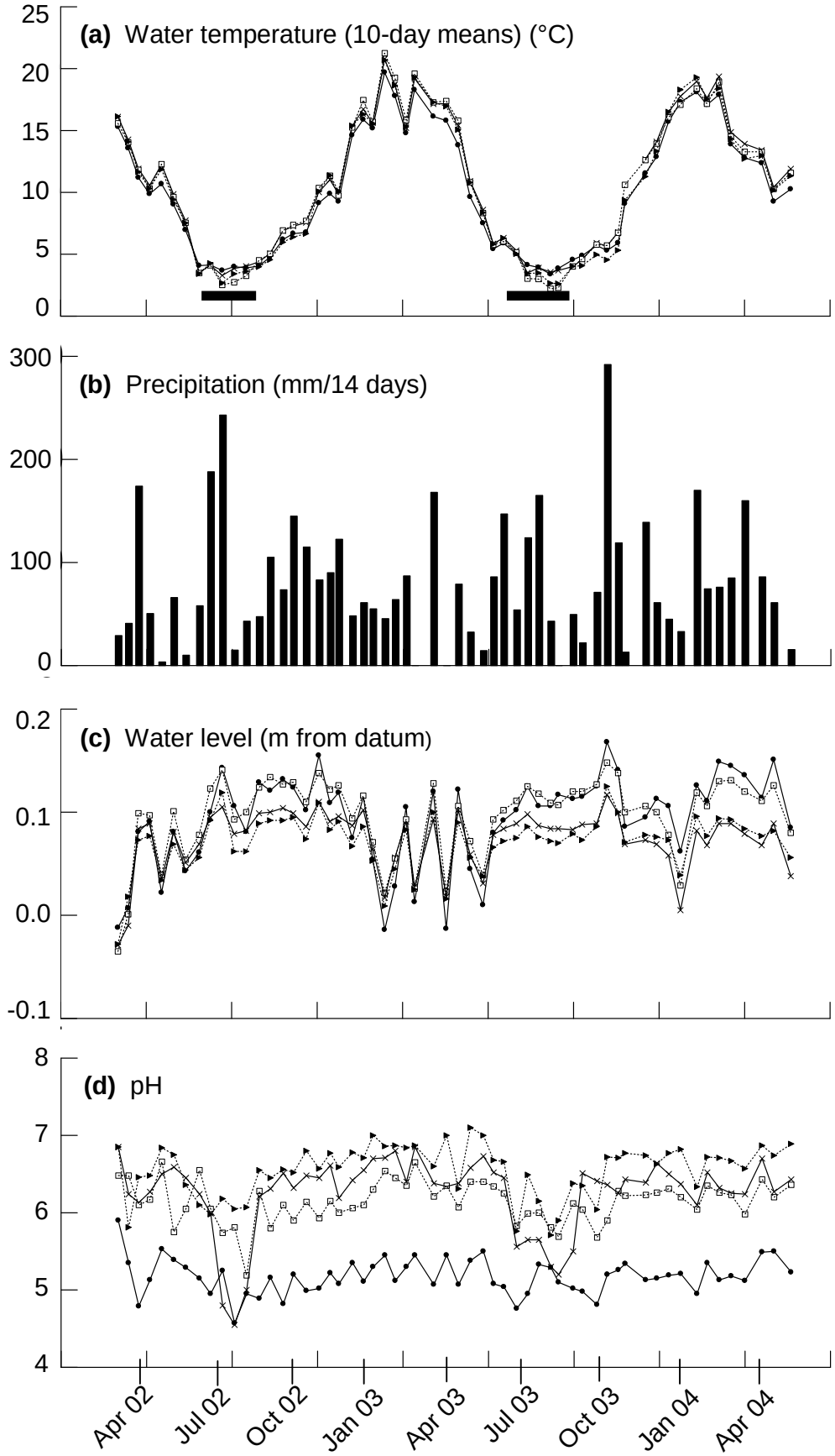


Figure III.2. Time series plots for 12 variables measured in four pools for up to 26 months.

● pool A, × pool B, □ pool C, ► pool D. Periods with ice cover are indicated by thick bars on plot (a).

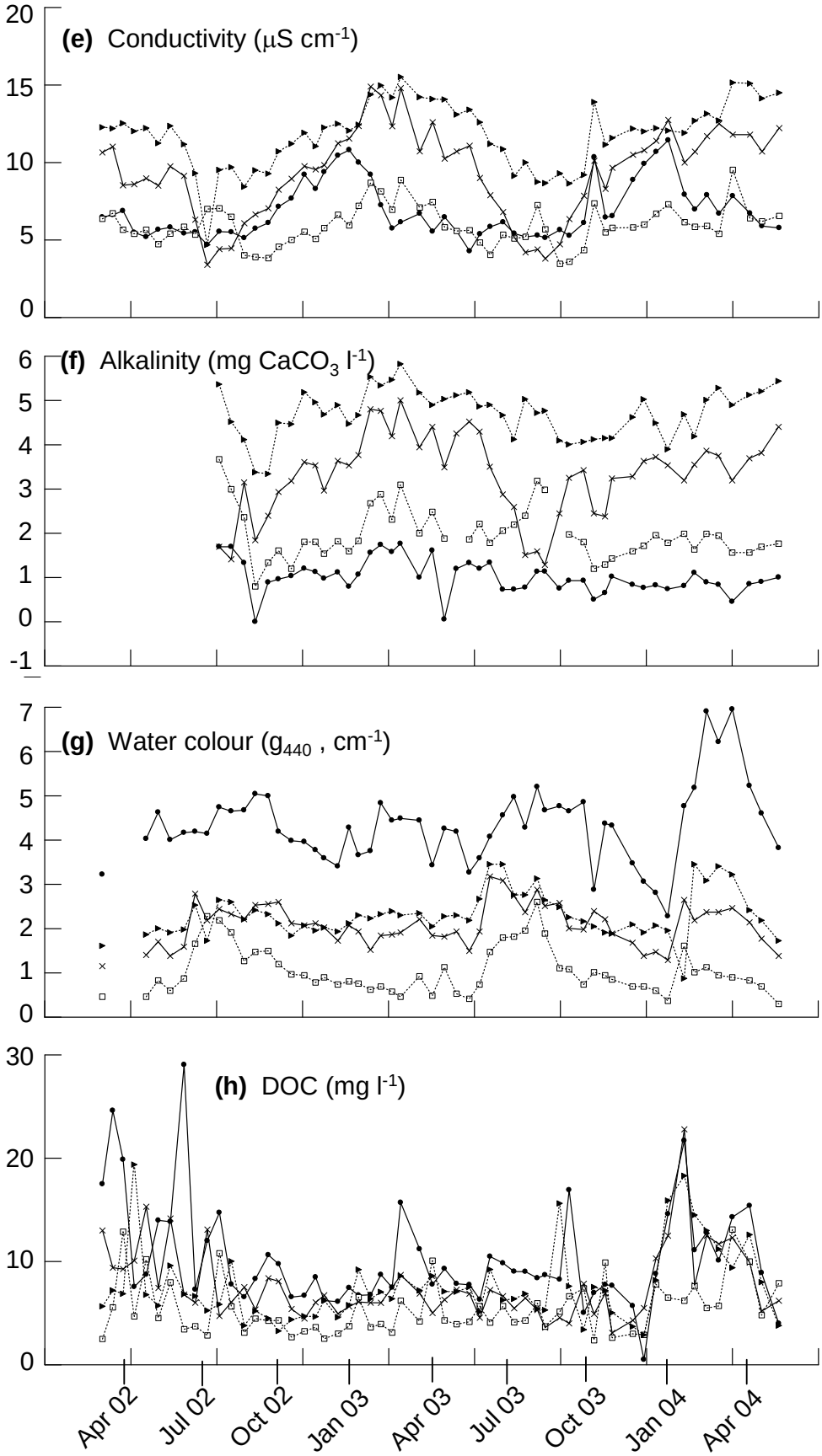


Figure III.2 (continued). Time series plots. ● pool A, × pool B, □ pool C, ► pool D. Periods with ice cover are indicated by thick bars on plot (a).

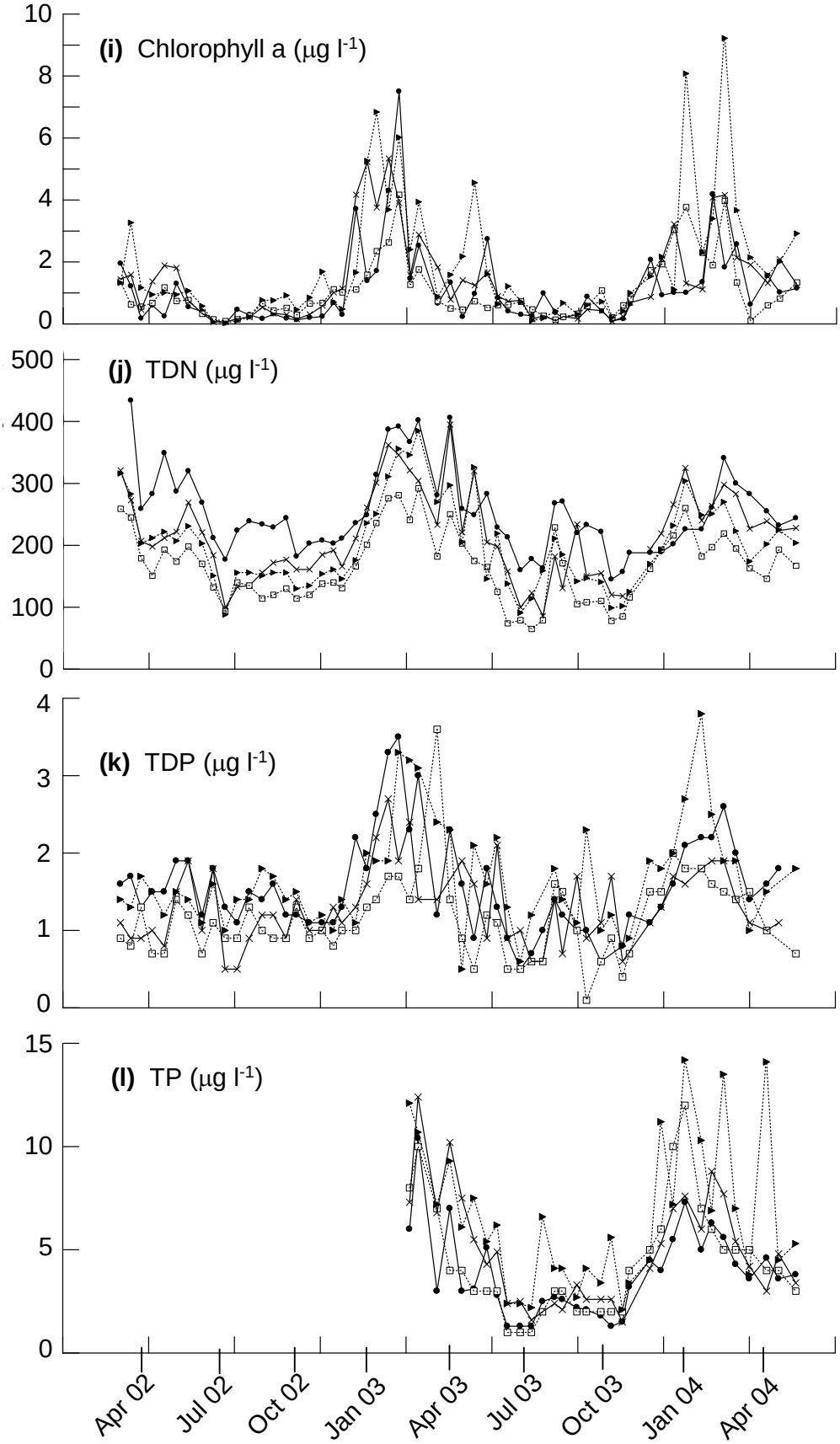


Figure III.2 (continued). Time series plots. ● pool A, × pool B, □ pool C, ► pool D. Periods with ice cover are indicated by thick bars on plot (a).

Table III.1. Basic statistics for physical and chemical variables measured at four pools in the Bealey Spur wetland area from February 2002 to April 2004. *n* = number of measurements from each pool. Different superscript letters following means at each pool indicate significant differences between pools (P < 0.05, Bonferroni-corrected).

			Means (standard deviation)				Coefficients of variation (%)	
Variable	Group	*n*	Pool A	Pool B	Pool C	Pool D	Within sites (range)	All pools combined
(a) Continuous measurements (15 min intervals)								
Temperature (°C)	physical	10.1 (5.5) (mean over sampling period)						
Rainfall (mm)		1800 mm p.a.						
(b) Physical measurements every 14 days (mean), for 26 months								
Water level change from datum (mm)	physical	57	92 (45)^{a}	76 (30)^{b}	96 (39)^{a}	71 (28)^{b}		
(c) Chemical / Nutrient / biological measurements every 14 days (mean), for 26 months								
pH	rainfall	57	5.17 (0.23)^{a}	6.25 (0.49)^{b}	6.14 (0.27)^{bc}	6.55 (0.34)^{d}	4 – 8	10
Conductivity (μS cm^{-1})	groundwater	57	6.9 (1.8)^{a}	9.3 (2.8)^{b}	5.9 (1.3)^{a}	11.8 (2.1)^{c}	18 – 31	36
Alkalinity (mg $CaCO_3$ l^{-1})	groundwater	51	1.01 (0.39)^{a}	3.30 (0.91)^{b}	1.98 (0.58)^{c}	4.72 (0.55)^{d}	12 – 38	56
Water colour (g440)	veg/recycling	55	4.32 (0.88)^{a}	2.08 (0.46)^{b}	1.04 (0.53)^{c}	2.31 (0.51)^{b}	20 – 51	55
Dissolved organic carbon (DOC) (mg l^{-1})	veg/recycling	57	10.27 (5.1)^{a}	7.65 (3.49)^{b}	5.41 (2.61)^{c}	7.55 (3.61)^{b}	46 – 49	54
Chlorophyll *a* (μg l^{-1})	biological	57	1.11 (1.31)^{a}	1.39 (1.35)^{ab}	1.05 (0.96)^{ab}	1.85 (2.00)^{b}	92 – 118	110
Dissolved silicon (mg l^{-1})	nutrient	57	0.43 (0.15)^{a}	0.31 (0.12)^{b}	0.31 (0.12)^{b}	0.41 (0.12)^{a}	29 – 39	38
NO_3-nitrogen (μg l^{-1})	nutrient	57	2.1 (0.8)	2.8 (2.5)	2.0 (1.6)	2.4 (2.0)	63 – 83	73
NH_4-nitrogen (μg l^{-1})	nutrient	57	7.6 (4.9)^{a}	5.7 (2.9)^{b}	4.7 (2.5)^{c}	5.8 (2.9)^{b}	23 – 54	45
Dissolved reactive phosphorus (DRP) (μg l^{-1})	nutrient	57	0.2 (0.3)^{a}	0.5 (0.6)^{bd}	0.3 (0.3)^{ab}	0.5 (0.6)^{cd}	99 – 118	119
Total dissolved nitrogen (TDN) (μg l^{-1})	nutrient	57	253 (67.5)^{a}	215 (71)^{b}	166 (57.5)^{c}	202 (70.4)^{b}	27 – 35	35

Variable	Group	*n*	Means (standard deviation) Pool A	Pool B	Pool C	Pool D	Coefficients of variation (%) Within sites (range)	All pools combined
Total dissolved phosphorus (TDP) (μg l^{-1})	nutrient	57	1.6 (0.6)^{ab}	1.4 (1.1)^{ac}	1.2 (0.6)^{c}	1.7 (0.8)^{b}	41 - 77	56
(d) Measurements every 14 days for 15 months								
Total nitrogen (TN) (μg l^{-1})	nutrient	32	286 (84)	296 (126.8)	221 (99.9)	294 (129.6)	29 – 45	35
Total phosphorus (TP) (μg l^{-1})	nutrient	32	3.8 (2.1)^{a}	4.9 (2.7)^{ab}	4.3 (2.8)^{a}	6.5 (3.6)^{b}	41 – 77	56
(e) Measurements every 2 months for 26 months								
Ca (mg l^{-1})	groundwater	15	0.43 (0.25)^{a}	0.89 (0.36)^{b}	0.46 (0.26)^{a}	1.58 (0.41)^{c}	26 – 58	68
Mg (mg l^{-1})	groundwater	15	0.09 (0.02)^{a}	0.14 (0.05)^{b}	0.09 (0.02)^{a}	0.13 (0.03)^{b}	18 – 35	34
Na (mg l^{-1})	rainfall	15	0.61 (0.32)^{a}	1.00 (0.46)^{b}	0.57 (0.23)^{a}	0.82 (0.28)^{ab}	34 – 53	49
K (mg l^{-1})	groundwater	15	0.07 (0.06)^{a}	0.13 (0.09)^{ab}	0.13 (0.09)^{ab}	0.18 (0.12)^{b}	66 – 87	78
SO_4 (mg l^{-1})	rainfall	15	0.03 (0.03)	0.06 (0.09)	0.04 (0.05)	0.05 (0.06)	120 - 147	145
Cl (mg l^{-1})	rainfall	15	0.86 (0.42)	1.02 (0.35)	1.03 (0.3)	1.03 (0.27)	26 – 50	35
Fe (mg l^{-1})	veg/recycling	15	0.05 (0.03)^{a}	0.02 (0.03)^{b}	0.01 (0.01)^{b}	0.01 (0.01)^{b}	57 - 205	122
Anion deficit (mEq l^{-1})	-	15	33.2 (10.7)	40.1 (31.2)	8.7 (18.1)	56.8 (27.0)	32 - 207	82

water temperature, conductivity, TDN and TDP (r = 0.427 – 0.766, P < 0.001); water colour and DOC (r = 0.408, P < 0.001).

Individual pools showed varying patterns though water level and rainfall were significantly related in all cases. The main differences among pools were that pools B and D in general showed patterns similar to the whole dataset, whereas pools A and C showed fewer correlations, with some pool-specific. For example, in pool C only, water colour was significantly inversely correlated with water temperature (r = 0.656, P < 0.001). Pool D differed from the whole dataset in that pH was not significantly correlated with water colour or alkalinity (though it was with temperature and conductivity).

In contrast to the whole dataset, water colour and DOC were not significantly related in any individual pool. Two variables (Si and NO_3) were unrelated to any others in all pools and in the combined dataset. Refer to Appendix IIIA (pages 74–78) for the complete correlation matrices.

Spatial and temporal patterns in water chemistry

Time-series plots (Figures III.2d-l, III.3) illustrate inconsistent variability and seasonal changes among both variables and pools, which were reflected in the analysis of temporal coherence (see below). For example pools B, C and D (but not pool A) showed winter minima in pH, which were most pronounced in pool B. Pool B also showed the most distinct seasonal fluctuations in conductivity and alkalinity. Winter maxima in water colour were recorded only in pool C. Late summer peaks in chlorophyll *a* reflected peaks in both TDN and TDP. Pools B and D (but not A and C) showed late winter minima in Ca, Mg, and anion deficit, especially in winter 2003 (Figure III.3a,b,f). Seasonal changes in Na, K and Cl were more uniform across pools (Figure III.3c,d,e). Anion deficit was unrelated to pH, DOC or water colour either across all pools and within individual pools.

Most variables showed significant inter-pool differences though only alkalinity was distinctive in all four pools (Table III.1). These differences were confirmed by the ANOSIM tests, which showed a significant global statistic for both the 12-variable and dissolved ion datasets (Table III.2). Pairwise comparisons showed that pool A was distinct from the other three pools, and pools B and D were most similar (Table III.2). Scrutiny of %CVs (Table III.1) indicates that within-pool variability (i.e., temporal) and across pool variability (spatial) were similar for most variables.

Between-pool differences in nutrient concentrations were less clear-cut than those of the chemical variables, with strong seasonal patterns in all four pools (summer maxima) (Figure III.2i–l), Table III.3). TN:TP ratios (by mass) ranged from 22 to 171, suggesting P limitation. Summer ratios were significantly lower than those in winter in all pools except pool D, due to relatively larger winter declines in TP (Figure III.2i, Table III.3). In all cases, TDN comprised mostly dissolved organic nitrogen (Table III.3).

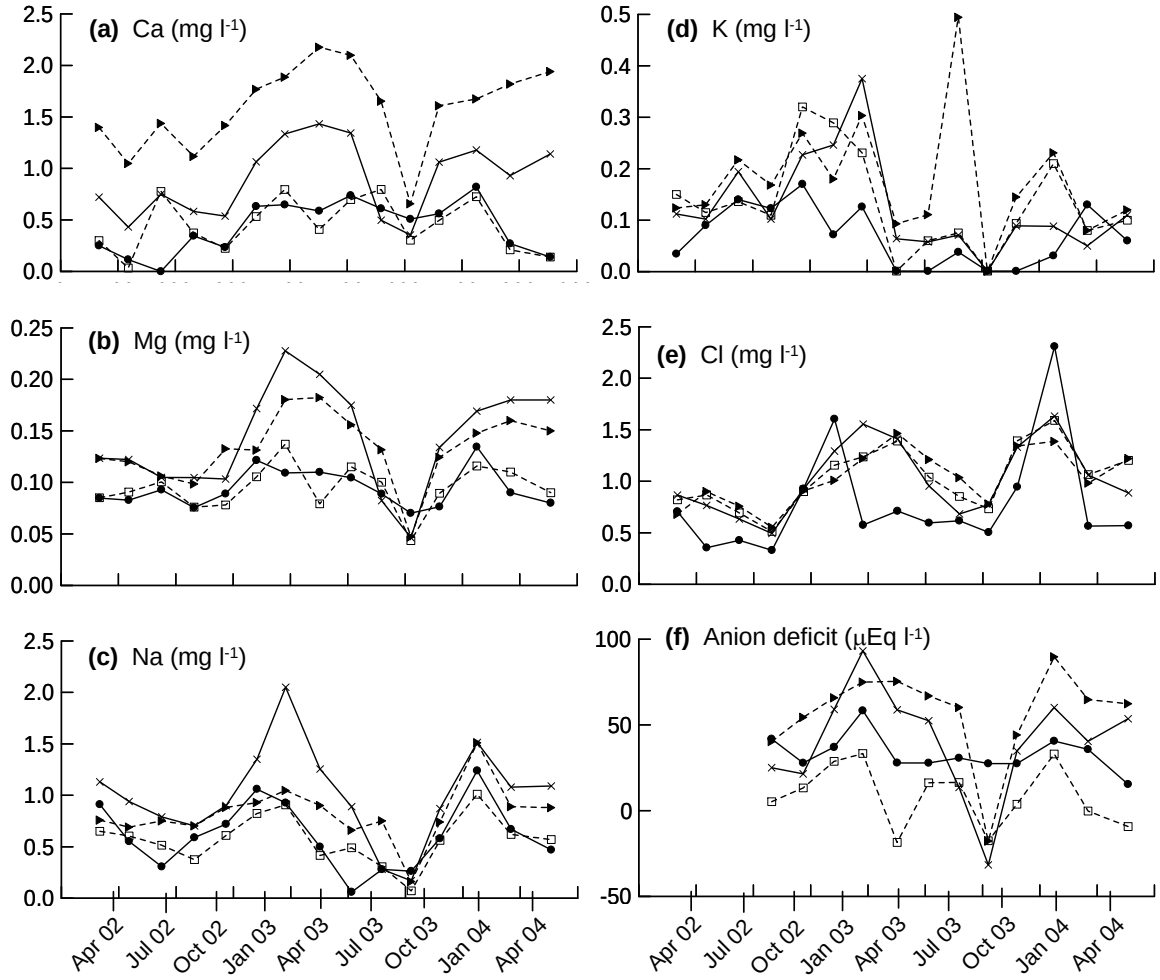


Figure III.3. Time series plots for major ions and anion deficit measured in four pools every 2 months for 26 months. ● pool A, × pool B, □ pool C, ► pool D.

Table III.2. Summary of spatial differences in chemical and nutrient variables across pool pairs. For nutrients, ANOSIM was run using NO_3, NH_4, DRP, TDN and TDP. Significance: ** P = 0.001; * P < 0.05. (Water temp. and level not included.)

		Pool pairs					
		A and B	A and C	A and D	B and C	B and D	C and D
One-way ANOSIM	Global R	Pairwise R					
12 variables (Table III.1c)	0.463**	0.552**	0.0.710**	0.720**	0.233**	0.099	0.481**
Dissolved ion variables (Table III.1e)	0.318**	0.290**	0.296**	0.602**	0.228**	0.109*	0.437**
Nutrients only (5 variables)	0.233**	0.259**	0.432**	0.341**	0.160**	0.040	0.183*
Number of significant differences (P < 0.05) between pools							
12 variables (Table III.1c)		9	7	9	6	5	10
Diss. ion variables (Table III.1e)		4	1	4	3	1	2
Total % different (of 19 variables)		68	42	68	47	32	63

Table III.3. Mean chlorophyll *a* and nutrient concentrations (with standard deviations) in summer and winter in the four pools. *n* = number of samples from each pool. All variables except TN : TP are in μg l^{-1}.

			Pool			
		n	**A**	**B**	**C**	**D**
Chlorophyll a	summer	21	2.05 (1.68)	2.73 (1.39)	1.79 (1.19)	3.46 (2.35)
	winter	13	0.37 (0.28)	0.24 (0.15)	0.31 (0.18)	0.39 (0.28)
TP	summer	14	5.4 (2.0)	6.8 (2.3)	6.6 (2.5)	9.5 (3.3)
	winter	6	2.2 (0.5)	2.3 0.6)	2.2 (0.8)	3.4 (0.9)
TN	summer	14	343 (84)	390 (101)	303 (81)	398 (97)
	winter	6	246 (51)	177 (52)	145 (67)	187 (48)
TN : TP (mass)	summer	14	67 (18)	58 (12)	48 (12)	45 (11)
	winter	6	113 (21)	75 (13)	66 (15)	50 (13)
TDP	summer	21	2.1 (0.6)	1.6 (0.5)	1.5 (0.6)	2.1 (0.8)
	winter	13	1.2 (0.3)	1.0 (0.4)	0.9 (0.4)	1.5 (0.4)
TDN	summer	20	301 (75.2)	276 (45.1)	219 (41.5)	263 (59.2
	winter	13	224 (35.1)	154 (43.6)	128 (43.5)	155 (34.1)
DRP	summer	21	0.3 (0.2)	0.5 (0.4)	0.3 (0.3)	0.7 (0.4)
	winter	13	0.3 (0.3)	0.4 (0.5)	0.4 (0.3)	0.3 (0.3)
NH_4	summer	21	7.3 (2.1)	5.3 (1.3)	4.7 (2.3)	5.6 (2.6)
	winter	13	7.2 (1.5)	7.3 (4.4)	5.2 (3.5)	6.5 (4.3)
NO_3	summer	21	2.1 (0.7)	2.2 (1.3)	1.6 (0.9)	2.3 (2.2)
	winter	13	2.4 (1.0)	3.5 (2.4)	2.4 (1.6)	3.2 (5.3)

Temporal coherence

Almost all variables showed positive correlations between pairs of pools (mean r = 0.58) with little variation among pool pairs (Table III.4). Out of 126 possible correlations, 89 (71%) were significant ($P < 0.05$), and 74 (59%) highly significant ($P < 0.01$). Highest mean coherence across all six pool pairs was for mean 10-day water temperature and water level ($r = 0.995$ and 0.93 respectively), followed by TDN ($r = 0.84$), Na ($r = 0.79$), Cl (r = 0.75) and chlorophyll *a* (r = 0.74). All six pool pairs were significantly correlated in all these cases, and also for water colour and Si ($P < 0.05$). The most striking inter-pool difference was in calcium, which was highly significantly correlated between pools A and C ($r = 0.90$), and B and D ($r = 0.872$) only Lowest overall coherence was for alkalinity ($r = 0.33$), SO_4 ($r = 0.34$) and DOC (0.37).

When variables were grouped on a physical – biological gradient, the rainfall and groundwater groups showed slightly higher mean coherences than the nutrient and vegetation groups, though means for individual variables covered wide ranges (Table III.4).

Table III.4. Summary of temporal coherence assessment. Refer to Table III.1 for assignment of variables to groups. The range given is for mean values across all pool pairs for individual variables in a group.

		Pool pairs						
	Overall mean	A and B	A and C	A and D	B and C	B and D	C and D	
Overall coherence								
All 21 variables	0.58	0.53	0.58	0.53	0.59	0.62	0.62	
%Significant (P<0.05)	71	67	67	47	81	81	71	
%Significant (P<0.01)	59	62	48	52	67	67	57	
Coherence by group								Range of values
Physical	0.96	0.93	0.96	0.97	0.98	0.96	0.98	0.93 – 0.995
Rainfall	0.61	0.37	0.70	0.64	0.58	0.53	0.83	0.34 – 0.79
Groundwater	0.53	0.49	0.62	0.39	0.46	0.70	0.50	0.33 – 0.69
Vegetation / recycling	0.45	0.45	0.28	0.37	0.62	0.60	0.37	0.36 – 0.52
Nutrients	0.51	0.55	0.47	0.49	0.53	0.46	0.56	0.39 – 0.84
Biological	0.74	0.78	0.67	0.67	0.75	0.79	0.77	0.74

Discussion

The combined results suggested that pools A and C, received more water from precipitation than pools B and D, which was consistent with observations on their locations within the mire (see "Study area", above). A broader range of water level change in pools A and C, compared to pools B and D (Table III.1, Figure III.2c) is consistent with direct rainwater inputs and drainage in an outward direction only, rather than recharge and drainage via subsurface flows (Bragg 2002). Calcium concentrations, which reflect groundwater inputs (Grieve et al. 1995), were significantly higher at pools B and D than at pools A and C (Table III.1). High temporal coherence for calcium between these pool pairs compared to the other four pairs also indicated their hydrological independence. Further, pools A and C were more similar to each other in ionic composition (except with respect to iron) than to pools B and D (Figure III.3b).

Rainfed (ombrotrophic) pools in mires are typically acidic as a result of a lack of inputs of bases (e.g., Ca^{2+}, Mg^{2+}) from groundwaters, and the accumulation of organic acids from peat decomposition and vegetation (e.g., *Sphagnum*) (Clymo 1987, Gorham et al. 1987). The transition from minerotrophy to ombrotrophy leads to two principal distributions of pH in Northern Hemisphere mires: waters buffered by the carbonate system (pH generally >6), and waters

dominated by dissolved humic material (pH generally <4.5) (Gorham et al. 1987). At Bealey, stronger intercorrelations between pH, alkalinity, conductivity and major groundwater cations (Ca, Mg) in pools B and D, than A and C again suggested that Pools B and D conformed to the first (minerotrophic) group, and pool A to the second (ombrotrophic). Despite similarity to pool A in cationic chemistry (and, presumably, water source), pool C was anomalous in that pH remained >6 for most of the year, yet conductivity and calcium were as low as in pool A.

A broad comparison of all four pools with mires from other regions may be drawn using a classification system developed in the Northern Hemisphere based on gradients of pH and calcium (Wheeler and Proctor 2000, Sjörs and Gunnarson 2002). A plot of log Ca vs. pH from open water mire pools shows that New Zealand data, including all those from the present study, overlap only marginally with two large datasets from northern Europe as a result of relatively high pH values for given calcium concentrations (Figure III.4). The Bealey data largely coincided with data from mire pools in Tasmania, and smaller datasets from Spain and Japan. Thus it seems that the anomalously high pH in pool C lies within a gradient shared by mire surface waters elsewhere.

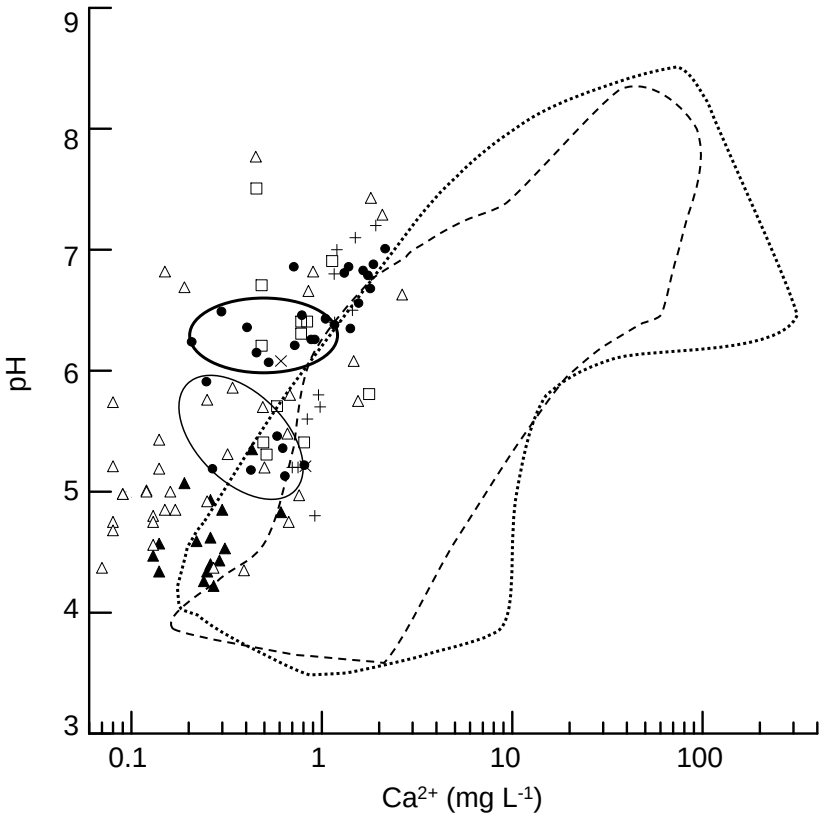


Figure III.4. pH values plotted against Ca concentrations (logged values) for the Bealey sites (●); other NZ data (Vanhoutte et al 2006 (Δ), Dickinson et al. 2002 (▲)); Tasmania (unpublished) (□); Spain (Muñoz et al. 2003 (+)); Japan (Watanabe et al. 2000 (×)). The extent of a UK/Ireland dataset (Wheeler and Proctor 2000) is enclosed by the dotted line, and a Swedish dataset (Sjörs and Gunnarsson 2002) by the dashed line. Only summer values are plotted from the present study to allow direct comparison with summer data from other studies. Data from pools A and C are circled by fine and bold lines, respectively.

One possible explanation for this discrepancy in pH is inter-Hemispheric variability in precipitation pH. We did not measure rainfall chemistry as part of the present study but data from a site within 10 km of the Bealey mire indicate relatively high pH and low Ca compared with European precipitation (Verhoeven et al. 1987, and see Table III.5). Although ombrotrophic mire surface waters are largely buffered against the effects of acid deposition (Gorham et al. 1984), Proctor and Maltby (1998) found that acid atmospheric pollution accounted for pH declines of up to 0.7 – 0.8 in some bog pools. However, the lack of such pollution in precipitation in New Zealand (Verhoeven et al. 1987) is unlikely to wholly explain the discrepancy in the Ca / pH relationship, because mire surface waters at unpolluted Northern Hemisphere sites have been estimated to have pH values around 4.4 (Proctor and Maltby 1998), which is less than the minimum values measured in the present study (pH 4.5, at sites A and B in winter 2002).

An alternative, and more likely, explanation for relatively high pH in mire waters is a lack of organic acids. The contribution of organic acids to the pH of surface waters has traditionally been assessed by determining the anion deficit: the surplus of cations (bases) over anions (acids), with the balance assumed to be from organic acids (e.g., Wilkinson et al. 1992). In mire waters, we expect the anion deficit to be high, and also expect a positive relationship between DOC and anion deficit. In present study, mean anion deficit was also very low (8 – 56 μEq l^{-1}). For example, anion deficits of 165 – 339 μEq l^{-1} have been reported from Finnish mire pools (Tahvanainen et al. 2002), with correspondingly higher mean DOC and pH values (DOC 12.4 – 56.6 mg l^{-1}, pH 6.2 – 3.97, compared with DOC 5.4 – 10.3 mg l^{-1}, pH 6.55 – 5.17 at Bealey). This strongly suggests that the relatively high pH values in the present study are a consequence of low levels of organic acids.

Table III.5. A selection of published pH and calcium concentrations (in μEq l^{-1}) in European ombrotrophic bog pools and rainwater compared with data from the present study.

Location	Rain		Bog pool		Reference
	Ca	pH	Ca	pH	
UK	21 – 42	-	54	3.5 – 4.3	Proctor 1992
UK	-	4.2 – 4.9	23 – 212	3.4 – 4.3	Proctor and Maltby 1998
Germany	50	4.2	-	-	Verhoeven et al. 1987
Italy	42	-	56	-	Bragazza 1994
New Zealand**	0.5 – 1.8	5.6 – 5.9	-	-	Verhoeven et al. 1987
New Zealand	4.0 – 11.8	4.9 – 5.7	-	-	Nichol et al. 1997
New Zealand	-	-	23, 24	5.2, 6.1	sites 1 and 3, this study*

*Sites 2 and 4 are not included in this comparison because these pools almost certainly receive lateral inputs. Mean Ca concentrations were, respectively, 44 and 79 μEq l^{-1}.

**Includes data from Craigieburn Range, ~10 km from Bealey, where rainfall pH = 5.9, Ca = 0.5 μEq l^{-1}.

Note also that the world median for DOC in bog waters is 30.3 mg l^{-1} (Wetzel 2001). Further, we found no correlations between anion deficit and DOC either within or across pools, which suggests that DOC contributes in inconsistent ways to the pH of each pool.

Vanhoutte et al. (2006a) reported relatively low overall water colour (and by inference low DOC) in small South Island, New Zealand, water bodies and attributed this to processes associated with high rainfall. While mean annual precipitation of 1800 mm at Bealey is not exceptionally high compared to other parts of New Zealand (e.g., see data in Vanhoutte et al. 2006a), it is considerably higher than that reported from mires in some parts of Europe (e.g., Bragazza and Gerdol 2002, Sjörs and Gunnarson 2002, Tahvanainen et al. 2002), but comparable to that in others (e.g., Proctor 2006). The relationship between rainfall and DOC release into surface waters is complex (Worrall et al. 2002), and there are also seasonal effects due to higher peat metabolism at higher temperatures (Bonnett et al. 2007). Therefore, lack of correlations between DOC and temperature or rainfall at Bealey makes it difficult to propose mechanisms. It is possible that turnover of DOC is high in this system, but a more focused study would be required to determine rates of release. It was interesting that relatively high values of DOC in all four pools between January and April 2004 (i.e. late summer) coincided with much higher rainfall than in summer 2003, which indicated enhanced release of DOC into the pools during rainfall. However, in the longer term, DOC depletion as a result of high rainfall could still be occurring (e.g., Worrall et al. 2002).

A further consideration is that DOC from different vegetation types could contribute to water acidity in different ways (e.g., Siegel et al. 2006). Most Northern Hemisphere mires are dominated by *Sphagnum* species, the DOC production and acidification properties of which have been studied (e.g., Clymo 1987). Although *Sphagnum* species are present in New Zealand mires (including at Bealey), peat is often formed from different vegetation types (Agnew et al. 1993, McQueen and Wilson 2000, Walker et al. 2001). The dominant species at Bealey is *Empodisma minus*, which is the main peat-forming species in ombrotrophic systems in New Zealand (Agnew et al. 1993). *E. minus* has been compared with other peat-forming species in New Zealand (Agnew et al. 1993, Clarkson et al. 2004), but information relative to Northern Hemisphere species is currently lacking. It is notable that mires in Tasmania, which appear to have a similar Ca / pH relationship as the New Zealand mires (Figure III.4), also have characteristic vegetation of “buttongrass moorland”, dominated by the sedge *Gymnoschoenus sphaerocephalus*.

We found both discrepancies and consistency in other spatio-temporal patterns between the study pools and those from elsewhere. For example, pH has been reported to be lower in summer than in winter in bog surface waters (Proctor 1994, 2006), whereas we generally found the opposite pattern at Bealey, even in the suspected ombrotrophic pool C. The pattern can be explained by the exceptionally low alkalinity in all pools. Winter pH reductions in pools B, C and D were therefore predictable in the absence of CO_2 removal from poorly buffered waters due to lack of primary production under the ice (Psenner 1989). In pool C only, in both winters, pH depression under the

ice was accompanied by increasing water colour, which could also have contributed to the winter pH decline in the form of organic acids (Glaser et al. 1981). Fluctuations in DOC over time and a lack of correlation between water colour and DOC suggested that organic substances were entering the water continuously but any coloured fraction was unstable when the pools were ice-free, most likely as a result of photodegradation and/or photobleaching (e.g., Wu et al. 2005).

Pool size may explain the difference in water colour between the presumed rain-fed pools A and C. A consequence of the small size of pool A is a high pool margin : water volume ratio, which would allow proportionately higher organic inputs at the peat margins than in larger pools such as pool C. This is consistent with the negative relationship between lake area and water colour found for larger water bodies (Rasmussen et al. 1989). Higher subsurface inputs into pools B and D would be expected to result in stronger humic coloration than in pool C.

We found no significant correlations between DOC and water colour at individual sites, though the relationship was clear across all pools. Mean long-term DOC and water colour were significantly correlated ($R^2 = 0.96$, $P = 0.013$, $n = 4$). Thus our data are consistent with previous findings of poor correlations between individual measurements of DOC and water colour, but strong correlations between long-term averages (Molot and Dillon 1997). Thus, the clear water in pool C is predictable from its lower mean DOC concentrations.

The seasonal patterns of dissolved ions at Bealey were similar to those reported over a bog – fen gradient in Canada (Vitt et al. 1995). Thus, there were summer peaks in Ca and Mg, which were most pronounced in the minerotrophic (i.e., fen) environments, and absent in the ombrotrophic environments. This was explained by higher evapo-concentration of ions in summer, which is muted in ombrotrophic pools by continuous cation exchange and lack of groundwater inputs. Interestingly, winter declines in Ca, Mg and anion deficit have been reported from ombrotrophic bog surface water in other regions (e.g. Proctor 1994, 2006), suggesting that regional variability exists. Lack of seasonal patterns in K, and little difference among pools at Bealey was consistent with reports from other areas (Vitt et al. 1995, Proctor 2006) and is explained by uptake of K by plants during the growing season.

The trophic status of lakes may be assessed using water column chlorophyll *a* or TP concentrations (Carlson 1977). All winter measurements of these parameters in our data set were consistent with oligotrophic or ultra-oligotrophic conditions. However, on the basis of maximum chlorophyll *a*, all four pools could be defined as approaching mesotrophic in summer, with maxima ranging from 4.2 to 9.2 $\mu g\ l^{-1}$. TN:TP ratios suggested P limitation at all times, based on a 7 : 1 ratio (by mass) in algal cells under balanced growth (Dodds and Priscu 1990). Higher ratios in winter resulted mainly from higher proportions of dissolved organic N (i.e., similar values of TN and TDN and very low NO_3 and NH_4, Table III.2) and may reflect a surplus of atmospheric inputs of dissolved organic nitrogen (Timperley et al. 1985) as a result of low biological activity. Overall, the four pools were much more homogeneous in terms of trophic status than in terms of ionic

chemistry, indicating independence of nutrient status from the Ca / pH gradient. This is consistent with conditions in other mire systems (Wheeler and Proctor 2000, Bragazza and Gerdol 2002).

In the present two-year study, the degree of temporal coherence of variables among pools helped to highlight between-pool differences. Most previous studies on temporal coherence have considered yearly time-scales (e.g., Magnuson et al. 1990, Baines et al. 2005), therefore comparisons with the present data have limited validity. Nevertheless, we found that coherence of multiple variables measured at two-week intervals over a series of seasons was similar to that reported interannually for some systems of larger lakes (Kling et al. 2000, George et al. 2000). A gradient of decreasing coherence spanning physical, rainfall, groundwater, and nutrient variables was also consistent with findings in earlier studies over annual timescales (Magnuson et al. 1990, George et al. 2000, Baines et al. 2000). In contrast to previous studies, the single biological variable considered, chlorophyll *a*, predictably fluctuated highly synchronously (i.e. seasonally) between all pool pairs.

We expected high temporal coherence of environmental variables between neighbouring water bodies across a succession of seasons. Therefore the variables which displayed lowest coherence are of most interest. Alkalinity had lowest overall coherence because of strong independence of patterns between pools B and C, which showed, respectively winter declines and elevations of alkalinity (Figure III.2f). We attribute the difference to hydrological factors. Thus, in ombrotrophic pool C, ice cover and lack of water inputs concentrate ions in the remaining liquid water, thus raising its buffering capacity. A similar elevation in alkalinity, which could have resulted from the same process, was seen during the largely dry period from January to April 2003 (compare Figures III.2b and III.2f). In contrast, in groundwater/runoff fed pool B (and, to a lesser extent, pool D), continuing and possibly enhanced surface inputs from periodic snowmelt are more likely to dilute the water beneath the ice, leading to a decline in alkalinity accompanying the pH decline.

Very low coherence for SO_4 between pool B and the other three pools compared with significant coherence across the remaining three pool pairs may not be significant since SO_4 was extremely low at all pools, often below detection limit. Third-lowest temporal coherence was found for DOC, in contrast to the relatively strong coherence of DOC across lakes over timescales of months recorded by Pace and Cole (2002). However, low synchrony of DOC in the present system was not unexpected, given significant inter-pool differences in water chemistry. In a peat landscape DOC inputs into freshwaters are influenced by hydrology and rainfall (Grieve et al. 1995, Worrall et al. 2002) but retention of DOC in water is limited by photodegradation, rates of which depend on multiple factors, in particular pH and alkalinity (Reche et al. 1999, Wu et al. 2005). Differential combinations of these variables would be expected to contribute to the unpredictable variability in DOC found in this study (Figure III.2h).

Extremely low alkalinity, with associated low conductivity and dissolved ion concentrations (in particular calcium and SO_4) sets apart the chemical environments of these mire pools from those in

many other freshwater systems. Although calcium and SO_4 in New Zealand river water and rainfall have been noted previously to be low by world standards (Close and Davies-Colley 1990, Verhoeven et al. 1987), the average values measured in the present study were exceptionally low. For example, they were one and two orders of magnitude lower, respectively, than average river waters in New Zealand (Smith and Maasdam 1994). Low-calcium mire pools and tarns described from other parts of the South Island (Vanhoutte et al. 2006a) also had exceptionally low SO_4, indicating some regional homogeneity in the water chemistry of these systems. The extreme ionic dilution of the Bealey mire pools also contrasts with the water chemistry of New Zealand's large pristine lakes. For example, mean concentrations of Na, Cl, K, Ca, and Mg in Lake Manapouri (South Island) are (in that order) 2 – 6 times the mean concentrations in the Bealey pools, and SO_4 is over 40 times greater (Reid et al. 1999). Ionic concentrations were also generally low compared with dilute freshwater systems in other parts of the world. For example, calcium and SO_4 concentrations in inland ponds and lakes of high Arctic Canada are, respectively, 20 and 60 times greater than those in the Bealey pools (Michelutti et al. 2002). Na and Cl concentrations are similar, presumably because of relative proximity of the New Zealand sites to the ocean.

In summary, this limnological dataset from a subalpine mire system in South Island, New Zealand adds to an extensive literature from the Northern Hemisphere on mire water chemistry. Our study has highlighted significant spatial and temporal heterogeneity of mire pool environments in a single small system. Spatial heterogeneity was expected given the contrasting water sources apparent from observations and even the pair of most similar pools (B and D) showed differences in variables such as pH and alkalinity, which could have biological implications. Temporal variability in many cases was at least as high as spatial variability. We also identified an overall divergence from described Northern Hemisphere mire-pool gradients arising from low calcium concentrations and relatively high pH. The latter is ascribed to unusually low concentrations of DOC in the study pools. The mechanisms leading to such low values are unclear, but could include the effects of high rainfall and associated flushing, and the influence of distinctive vegetation types. Low buffering capacities resulted in marked water chemistry changes in winter, particularly under ice, except in waters buffered by humic material. Despite the within and between-pool variability of these mire pools, their average water chemistry is very different from that typical in rivers and lakes in New Zealand, and from that in comparable small water bodies in other parts of the world. Clearly, many of the variables measured affect biological processes and may constrain the community structure of aquatic biota. Given the known prevalence of endemic diatoms in bogs and tarns in New Zealand (Kilroy et al. 2007 [I]), more detailed biological studies on these systems are warranted.

APPENDIX IIIA Pearson correlation matrices generated across all sites, and at individual sites, with Bonferroni-corrected significance indicated in bold type ($P < 0.001$), underlined ($P < 0.01$), or italic underlined ($P < 0.05$). Correlations were run using all data available for each pair of variables. Refer to Table 1 for *n* applicable to each variable. MT = mean water temperature.

ALL SITES

	PH	COND	ALK49	G440	DOC	CHL	SI	NO3	NH4	DRP	TDN	TDP	PN	PP	TN	TP	MT_24
PH	1.000																
COND	**0.600**	1.000															
ALK49	**0.793**	**0.777**	1.000														
G440	**-0.662**	-0.099	-0.340	1.000													
DOC	-0.220	0.073	-0.050	**0.408**	1.000												
CHL	**0.400**	**0.506**	0.339	-0.109	0.102	1.000											
SI2	-0.139	0.041	0.052	0.290	0.045	-0.052	1.000										
NO3	-0.029	0.051	0.048	0.034	-0.077	-0.050	0.101	1.000									
NH4	-0.276	0.043	-0.099	**0.391**	0.124	-0.081	0.127	0.239	1.000								
DRP	*0.252*	**0.351**	**0.392**	-0.079	-0.026	0.176	-0.001	0.246	**0.485**	1.000							
TDN	-0.022	**0.332**	0.101	0.293	**0.368**	**0.557**	0.079	-0.009	*0.256*	0.235	1.000						
TDP	0.134	**0.392**	0.272	0.138	0.167	**0.447**	0.117	0.034	0.240	**0.482**	**0.638**	1.000					
PN	**0.508**	**0.554**	**0.460**	-0.239	0.167	**0.748**	0.092	-0.148	-0.126	0.235	**0.537**	0.389	1.000				
PP	**0.471**	**0.535**	**0.422**	-0.234	0.236	**0.748**	0.077	-0.142	-0.121	0.185	**0.512**	**0.427**	**0.912**	1.000			
TN	0.237	**0.469**	0.297	0.074	0.315	**0.710**	0.114	-0.062	0.040	0.273	**0.912**	**0.611**	**0.835**	**0.776**	1.000		
TP	**0.454**	**0.562**	**0.450**	-0.189	0.253	**0.721**	0.093	-0.112	-0.048	*0.346*	**0.620**	**0.673**	**0.866**	**0.948**	**0.824**	1.000	
MT_24H	**0.320**	**0.441**	0.166	-0.177	0.109	**0.753**	-0.098	-0.163	-0.099	0.154	**0.620**	**0.427**	**0.668**	**0.692**	**0.717**	**0.707**	1.000
MT_10D	**0.318**	**0.462**	0.162	-0.162	0.180	**0.766**	-0.094	-0.116	-0.098	0.151	**0.642**	**0.488**	**0.680**	**0.696**	**0.750**	**0.730**	**0.918**
RAIN1D	0.001	-0.005	-0.075	0.023	-0.055	-0.097	0.064	0.046	-0.003	-0.080	-0.130	-0.039	0.026	0.008	0.016	0.015	-0.125
RAIN15D	-0.037	-0.019	-0.106	0.102	0.022	-0.076	0.087	-0.162	-0.111	-0.114	-0.292	-0.128	-0.073	-0.036	-0.214	-0.086	-0.074
LEVEL	**-0.357**	**-0.366**	**-0.479**	0.210	-0.140	**-0.397**	0.085	0.099	-0.034	-0.151	**-0.544**	*-0.275*	**-0.461**	**-0.427**	**-0.503**	**-0.456**	**-0.461**
NA	0.385	**0.725**	0.442	-0.176	0.209	0.578	-0.002	0.012	-0.058	0.236	*0.506*	0.407	0.707	*0.663*	0.710	**0.765**	**0.648**
CA	**0.578**	**0.827**	**0.852**	-0.097	-0.067	0.302	0.083	-0.006	0.095	0.445	0.178	0.448	0.456	0.375	0.362	0.524	0.187
K	0.302	0.314	0.368	-0.177	-0.258	0.195	0.170	-0.139	-0.155	0.279	0.005	0.237	0.287	0.297	0.124	0.436	0.178
MG	*0.478*	**0.818**	**0.658**	-0.172	0.039	*0.485*	0.072	0.137	0.052	0.366	0.480	*0.489*	0.502	0.421	0.588	0.596	0.474
CL	0.303	0.537	0.175	-0.321	0.020	0.430	-0.190	0.058	0.089	0.348	0.216	0.265	0.581	0.565	0.496	0.606	**0.611**
SO4	0.115	-0.058	0.089	-0.046	-0.305	-0.304	-0.079	0.171	-0.048	0.092	-0.262	-0.088	-0.190	-0.190	-0.143	-0.109	-0.153
Fe	-0.573	-0.122	-0.363	**0.636**	0.227	0.053	0.087	-0.105	0.445	0.161	0.196	0.196	-0.166	-0.156	-0.031	-0.102	-0.050

	MT_10D	R1D	R15D	LEVEL	NA	CA	K	MG	CL	SO4	Fe
MT_10D	1.000										
RAIN_1D	0.016	1.000									
RAIN_15D	-0.035	**0.337**	1.000								
LEVEL	**-0.379**	**0.462**	**0.527**	1.000							
NA	**0.669**	-0.039	-0.073	-0.386	1.000						
CA	0.205	-0.094	-0.097	-0.219	0.468	1.000					
K	0.114	-0.098	0.335	0.039	*0.475*	0.316	1.000				
MG	0.522	-0.095	-0.205	-0.315	**0.807**	**0.724**	0.359	1.000			
CL	**0.594**	-0.065	-0.263	-0.177	0.571	0.375	0.150	0.521	1.000		
SO4	-0.263	0.055	0.237	0.153	-0.114	-0.052	0.016	-0.182	-0.142	1.000	
FE	-0.075	0.018	0.176	0.184	-0.067	-0.058	-0.174	-0.040	0.026	-0.194	1.000

SITE 1

	PH	COND	ALK49	G440	DOC	CHL	SI	NO3	NH4	DRP	TDN	TDP	PN	PP	TN
PH	1.000														
COND	0.020	1.000													
ALK49	0.097	-0.207	1.000												
G440	-0.252	-0.366	-0.108	1.000											
DOC	0.033	-0.165	-0.023	0.237	1.000										
CHL	0.463	0.256	0.383	0.007	0.021	1.000									
SI2	-0.232	-0.306	0.148	0.141	-0.001	-0.261	1.000								
NO3	-0.036	-0.049	-0.171	0.002	-0.206	-0.061	-0.378	1.000							
NH4	-0.016	0.140	-0.123	-0.128	-0.063	-0.147	-0.292	0.278	1.000						
DRP	-0.005	0.088	0.057	-0.029	-0.063	0.038	-0.315	0.264	**0.703**	1.000					
TDN	0.400	-0.121	0.526	0.216	0.276	*0.531*	-0.154	-0.141	-0.017	0.032	1.000				
TDP	0.425	0.205	0.368	0.048	0.109	**0.722**	-0.114	-0.149	-0.172	-0.085	**0.731**	1.000			
PN	0.589	0.208	0.527	-0.120	0.179	**0.784**	0.091	-0.163	-0.241	-0.183	0.624	**0.797**	1.000		
PP	0.509	0.293	0.482	-0.181	0.267	0.717	0.054	-0.185	-0.155	-0.127	*0.625*	**0.796**	**0.953**	1.000	
TN	0.481	-0.142	*0.637*	0.198	0.245	*0.627*	0.122	-0.151	-0.115	-0.006	**0.972**	**0.836**	**0.791**	**0.778**	1.000
TP	0.525	0.248	0.482	-0.089	0.311	**0.747**	0.051	-0.182	-0.160	-0.132	0.697	**0.885**	**0.948**	**0.985**	**0.833**
MT_24H	0.395	0.537	0.266	-0.102	0.044	**0.751**	-0.308	-0.139	-0.076	-0.008	0.574	**0.687**	**0.792**	**0.837**	*0.644*
MT_10D	0.391	0.539	0.133	-0.053	0.113	**0.717**	-0.335	-0.108	-0.081	-0.008	0.565	**0.724**	0.705	**0.766**	*0.648*
R1D	-0.018	0.036	-0.341	0.087	-0.071	-0.156	0.080	-0.063	0.212	0.145	-0.115	-0.052	-0.229	-0.205	-0.012
R15D	-0.195	0.259	-0.358	0.201	0.098	-0.097	0.191	-0.313	0.061	-0.047	-0.423	-0.199	-0.304	-0.249	-0.410
LEVEL	-0.512	0.104	*-0.589*	0.396	-0.201	-0.470	0.159	0.127	0.148	0.100	-0.666	-0.459	-0.550	-0.589	-0.521
NA	0.303	*0.838*	0.024	-0.316	0.255	0.471	-0.130	-0.238	-0.398	0.080	0.196	0.566	0.873	0.775	0.321
CA	-0.018	0.435	0.115	-0.316	0.157	0.409	-0.247	-0.300	0.442	0.362	-0.000	0.187	0.122	0.339	-0.116
K	-0.393	0.059	0.127	0.435	-0.336	-0.021	0.557	-0.162	-0.387	-0.189	0.075	0.230	0.255	-0.039	0.149
MG	0.102	0.764	0.161	-0.517	-0.039	0.472	-0.083	-0.316	0.187	0.153	0.243	0.663	0.791	0.858	0.468
CL	0.129	0.784	-0.478	-0.312	0.016	0.288	-0.498	0.198	-0.438	0.044	-0.272	0.137	0.592	0.462	0.010
SO4	0.162	-0.022	0.129	0.044	-0.105	-0.205	-0.043	-0.174	-0.293	-0.246	-0.203	-0.120	-0.190	-0.149	-0.329
IRON	-0.494	-0.032	-0.151	0.635	0.102	0.175	0.017	-0.420	0.350	0.430	-0.057	-0.016	-0.341	-0.358	-0.151

	TP	MT_24H	MT_10D	RAIN_1D	RAIN_15D	LEVEL	NA	CA	K	MG	CL	SO4	FE
TP	1.000												
MT_24	**0.839**	1.000											
MT_10D	**0.805**	**0.915**	1.000										
RAIN_1D	-0.129	-0.131	0.012	1.000									
RAIN_15D	-0.252	-0.048	-0.023	0.336	1.000								
LEVEL	-0.531	-0.454	-0.350	0.484	*0.530*	1.000							
NA	0.755	0.786	0.770	0.196	0.063	-0.305	1.000						
CA	0.246	0.300	0.282	-0.018	0.004	-0.118	0.203	1.000					
K	0.053	0.002	-0.073	0.164	0.416	0.318	0.219	-0.564	1.000				
MG	0.836	0.595	0.634	-0.052	-0.072	-0.346	0.571	0.586	-0.063	1.000			
CL	0.439	0.484	0.448	0.240	-0.087	0.101	0.557	0.370	-0.236	0.459	1.000		
SO4	-0.187	0.127	-0.088	-0.174	0.332	-0.085	0.153	-0.253	0.141	-0.272	0.033	1.000	
FE	-0.340	-0.150	-0.212	0.669	0.615	0.594	-0.194	0.323	0.054	-0.008	-0.030	-0.193	1.000

SITE 2

	PH	COND	ALK49	G440	DOC	CHL	SI	NO3	NH4	DRP	TDN	TDP	PN	PP	TN
PH	1.000														
COND	**0.769**	1.000													
ALK49	**0.782**	**0.866**	1.000												
G440	*-0.514*	-0.555	-0.596	1.000											
DOC	0.078	0.180	0.150	-0.097	1.000										
CHL	0.569	0.779	**0.697**	-0.453	0.176	1.000									
SI2	-0.050	-0.041	0.079	0.093	-0.246	-0.183	1.000								
NO3	-0.082	0.003	0.125	0.081	-0.230	-0.168	0.380	1.000							
NH4	-0.083	-0.110	-0.111	0.283	-0.203	-0.184	0.182	0.367	1.000						
DRP	0.139	0.281	0.322	-0.047	-0.174	0.119	0.111	0.244	**0.631**	1.000					
TDN	0.552	**0.798**	**0.734**	*-0.517*	0.240	**0.683**	0.015	0.014	0.113	0.455	1.000				
TDP	0.358	0.508	0.496	-0.190	-0.016	0.356	0.002	0.122	0.314	**0.713**	**0.703**	1.000			
PN	0.502	0.615	0.597	-0.367	0.189	*0.659*	0.289	-0.223	-0.189	0.158	0.547	0.192	1.000		
PP	0.514	0.676	0.597	-0.401	0.365	**0.809**	0.153	-0.267	-0.285	0.069	0.612	0.217	**0.949**	1.000	
TN	0.544	**0.774**	0.730	-0.469	0.301	0.729	0.280	-0.067	-0.125	0.350	**0.891**	0.530	**0.868**	**0.878**	1.000
TP	0.492	0.727	*0.663*	-0.419	0.291	0.717	0.183	-0.130	-0.095	0.426	**0.825**	*0.669*	**0.821**	**0.858**	**0.936**
MT_24H	0.578	**0.845**	**0.705**	*-0.523*	0.265	**0.799**	-0.014	-0.179	-0.083	0.273	**0.781**	0.427	0.631	0.744	**0.801**
MT_10D	0.585	**0.869**	**0.716**	-0.456	0.356	**0.846**	-0.063	-0.113	-0.078	0.247	**0.809**	0.504	0.666	**0.790**	**0.830**
RAIN_1D	0.040	-0.001	-0.038	0.154	0.052	-0.063	0.042	0.121	-0.052	-0.103	-0.159	-0.066	0.058	0.072	0.006
RAIN_15D	0.026	-0.093	-0.157	0.382	0.110	-0.047	-0.223	-0.275	-0.066	-0.205	-0.283	-0.238	0.006	0.074	-0.159
LEVEL	-0.320	-0.478	*-0.531*	**0.636**	-0.255	-0.356	-0.023	0.078	-0.067	-0.207	**-0.636**	-0.242	-0.407	-0.391	-0.578
NA	0.533	0.885	0.705	-0.427	0.204	0.738	0.216	-0.023	-0.204	0.142	0.791	0.374	0.777	0.689	0.932
CA	0.270	0.742	0.766	-0.239	-0.236	0.421	0.285	0.315	0.037	0.416	0.699	0.667	0.471	0.335	0.752
K	0.275	0.372	0.320	0.081	-0.100	0.495	0.187	-0.237	-0.301	-0.140	0.196	-0.016	0.532	0.533	0.442
MG	0.371	0.890	0.796	-0.321	0.053	0.689	0.236	0.253	-0.163	0.252	0.768	0.532	0.529	0.427	0.806
CL	0.390	0.808	0.508	-0.394	-0.056	0.554	0.140	-0.022	0.137	0.417	0.762	0.500	0.751	0.670	0.939
SO4	-0.031	-0.229	-0.068	0.348	-0.371	-0.298	-0.048	0.254	0.566	0.448	-0.126	0.168	-0.370	-0.348	-0.116
FE	-0.444	-0.178	-0.482	0.139	-0.273	-0.043	-0.192	-0.239	0.304	0.245	-0.129	0.069	-0.375	-0.332	-0.475

	TP	MT_24H	MT_10D	RAIN_1D	RAIN_15D	LEVEL	NA	CA	K	MG	CL	SO4	FE
TP	1.000												
MT_24	**0.795**	1.000											
MT_10D	**0.846**	**0.918**	1.000										
RAIN_1D	0.044	-0.119	0.014	1.000									
RAIN_15D	-0.150	-0.083	-0.042	0.340	1.000								
LEVEL	-0.521	-0.546	-0.466	*0.528*	0.590	1.000							
NA	0.781	*0.857*	*0.855*	-0.115	-0.219	-0.444	1.000						
CA	0.759	0.528	0.599	-0.164	-0.478	-0.288	0.712	1.000					
K	0.221	0.466	0.340	-0.063	0.315	0.122	0.667	0.224	1.000				
MG	0.720	0.731	0.775	-0.054	-0.442	-0.332	0.879	0.893	0.419	1.000			
CL	0.896	0.836	0.830	-0.055	-0.241	-0.385	0.766	0.748	0.327	0.728	1.000		
SO4	-0.039	-0.213	-0.266	0.463	0.069	0.337	-0.460	-0.305	-0.347	-0.401	-0.137	1.000	
FE	-0.197	-0.030	-0.045	-0.235	0.145	0.079	-0.084	0.132	-0.032	0.003	0.241	-0.143	1.000

SITE 3

	PH	COND	ALK49	G440	DOC	CHL	SI	NO3	NH4	DRP	TDN	TDP	PN	PP	TN
PH	1.000														
COND	0.225	1.000													
ALK49	-0.096	0.388	1.000												
G440	**-0.664**	-0.181	0.373	1.000											
DOC	0.054	0.227	0.156	-0.073	1.000										
CHL	0.468	0.277	-0.020	-0.529	-0.051	1.000									
SI2	0.144	-0.157	-0.205	-0.171	0.016	0.174	1.000								
NO3	-0.109	0.069	-0.111	0.026	-0.048	-0.094	0.215	1.000							
NH4	-0.091	0.181	0.203	0.195	-0.013	-0.018	0.100	0.185	1.000						
DRP	0.105	0.284	0.297	-0.008	0.029	0.058	0.179	*0.420*	0.495	1.000					
TDN	*0.498*	**0.624**	0.374	-0.469	0.117	**0.610**	-0.016	-0.105	0.075	0.266	1.000				
TDP	0.080	*0.506*	0.212	-0.161	0.017	0.379	0.150	0.180	0.110	0.404	0.587	1.000			
PN	0.504	0.526	0.122	-0.498	0.105	**0.764**	-0.003	-0.242	-0.037	0.155	**0.768**	0.504	1.000		
PP	0.452	0.514	0.093	-0.474	0.100	**0.757**	-0.026	-0.224	-0.002	0.185	**0.744**	0.505	**0.990**	1.000	
TN	0.486	0.611	0.308	-0.444	0.128	*0.658*	-0.017	-0.141	0.039	0.250	**0.957**	*0.642*	**0.921**	**0.902**	1.000
TP	0.433	0.581	0.114	-0.438	0.095	0.709	-0.016	-0.160	-0.013	0.251	**0.788**	0.681	**0.956**	**0.966**	**0.913**
MT_24	**0.595**	*0.513*	-0.024	**-0.656**	0.065	**0.802**	0.062	-0.229	-0.141	0.006	**0.741**	0.409	**0.814**	**0.782**	**0.799**
MT_10D	0.567	0.537	-0.057	**-0.630**	0.099	**0.769**	0.103	-0.170	-0.114	0.009	**0.765**	0.521	**0.771**	**0.751**	**0.802**
RAIN_1D	-0.133	-0.088	-0.366	0.086	-0.303	-0.148	0.016	0.092	-0.122	-0.243	-0.169	0.052	-0.035	-0.044	-0.024
RAIN_15D	-0.148	-0.101	-0.403	0.251	-0.289	-0.016	0.112	-0.032	-0.193	-0.143	-0.336	-0.032	-0.005	0.007	-0.197
LEVEL	-0.558	-0.412	-0.429	*0.502*	-0.114	-0.343	0.167	0.204	-0.134	-0.114	**-0.694**	-0.099	-0.556	-0.533	-0.607
NA	0.290	0.750	-0.087	-0.511	-0.147	0.789	0.303	-0.148	0.308	0.146	0.666	0.746	0.845	0.845	0.787
CA	-0.411	0.244	0.496	0.417	-0.361	0.084	-0.004	0.127	0.410	0.714	-0.006	0.378	0.228	0.246	0.021
K	-0.080	0.330	-0.323	-0.116	-0.509	0.424	0.160	-0.220	-0.088	-0.080	0.192	0.370	0.751	0.794	0.554
MG	0.195	0.596	0.307	-0.129	-0.118	0.547	0.242	-0.048	0.444	0.303	0.419	0.769	0.443	0.444	0.373
CL	0.120	0.751	-0.122	-0.588	0.266	0.559	0.184	0.003	0.517	0.347	0.523	0.496	0.743	0.711	0.791
SO4	-0.063	-0.307	-0.579	0.295	-0.429	-0.378	-0.012	0.177	-0.407	-0.032	-0.339	-0.115	-0.089	-0.059	-0.201
FE	-0.369	0.026	0.069	0.454	-0.070	-0.225	-0.546	-0.032	0.340	0.243	-0.299	-0.152	-0.146	-0.105	-0.276

	TP	MT_24	MT_10D	RAIN_1D	RAIN_15D	LEVEL	NA	CA	K	MG	CL	SO4	FE
TP	1.000												
MT_24	**0.769**	1.000											
MT_10D	**0.787**	**0.923**	1.000										
RAIN_1D	0.020	-0.094	0.032	1.000									
RAIN_15D	0.017	-0.066	-0.029	0.336	1.000								
LEVEL	-0.470	*-0.505*	-0.437	0.460	0.591	1.000							
NA	0.873	0.699	0.734	-0.088	0.025	-0.429	1.000						
CA	0.279	-0.115	-0.088	-0.275	0.403	0.104	0.214	1.000					
K	0.804	0.373	0.287	0.001	0.344	-0.071	0.715	0.129	1.000				
MG	0.502	0.351	0.426	-0.175	0.152	-0.136	0.749	0.568	0.381	1.000			
CL	0.741	0.690	0.702	-0.224	-0.399	-0.359	0.593	0.204	0.122	0.467	1.000		
SO4	-0.047	-0.238	-0.365	-0.281	0.383	0.182	-0.067	-0.108	0.257	-0.236	-0.366	1.000	
FE	-0.075	-0.192	-0.217	-0.307	0.158	0.106	-0.204	0.418	-0.233	0.048	0.210	-0.085	1.000

SITE 4

	PH	COND	ALK49	G440	DOC	CHL	SI	NO3	NH4	DRP	TDN	TDP	PN	PP	TN
PH	1.000														
COND	**0.609**	1.000													
ALK49	0.221	0.627	1.000												
G440	-0.282	-0.028	0.071	1.000											
DOC	0.061	0.206	-0.028	0.141	1.000										
CHL	*0.504*	**0.613**	0.336	0.028	0.298	1.000									
SI2	0.050	0.147	0.097	0.153	-0.167	0.030	1.000								
NO3	0.062	0.107	0.139	0.016	-0.003	0.058	0.190	1.000							
NH4	-0.029	0.094	0.162	0.255	0.057	0.011	0.040	0.176	1.000						
DRP	0.135	0.278	0.291	0.145	0.203	0.225	0.019	0.141	0.568	1.000					
TDN	0.386	**0.604**	0.506	-0.077	0.269	**0.719**	0.057	0.013	0.216	0.307	1.000				
TDP	0.220	0.212	0.230	-0.014	0.254	0.355	0.049	-0.099	0.360	**0.621**	0.574	1.000			
PN	0.509	0.586	0.357	-0.174	0.371	**0.848**	-0.054	-0.103	-0.050	0.162	**0.796**	0.355	1.000		
PP	0.436	0.541	0.317	-0.211	0.386	0.701	0.016	-0.031	-0.048	0.113	*0.647*	0.328	**0.887**	1.000	
TN	0.484	0.575	0.477	-0.152	0.333	**0.805**	-0.012	-0.062	0.062	0.250	**0.957**	0.514	**0.937**	**0.797**	1.000
TP	0.415	0.499	0.359	-0.234	0.411	0.677	0.008	-0.082	0.040	0.302	0.722	0.558	**0.872**	**0.965**	**0.833**
MT_24	**0.594**	**0.678**	0.390	-0.195	0.200	**0.757**	-0.064	-0.110	-0.067	0.244	**0.718**	0.350	**0.748**	0.677	**0.746**
MT_10D	0.565	**0.733**	0.437	-0.173	0.323	**0.804**	-0.002	-0.081	-0.093	0.249	**0.767**	0.385	**0.821**	0.724	**0.823**
RAIN_1D	0.059	-0.011	-0.137	-0.128	0.020	-0.054	0.145	0.005	-0.006	-0.114	-0.139	-0.090	0.148	0.106	0.073
RAIN_15D	-0.080	-0.143	-0.242	0.129	0.063	-0.132	0.272	-0.112	-0.252	-0.072	-0.270	-0.061	-0.140	-0.050	-0.192
LEVEL	-0.217	-0.317	-0.370	0.136	-0.024	-0.325	0.074	0.087	-0.124	-0.103	**-0.592**	-0.176	-0.333	-0.180	-0.412
NA	0.422	0.507	0.119	-0.117	0.529	0.735	-0.014	0.050	0.027	0.297	0.527	0.127	0.823	0.842	0.788
CA	0.386	0.742	0.671	0.184	0.102	0.384	0.170	0.317	0.341	0.430	0.418	0.214	0.394	0.336	0.473
K	-0.317	-0.075	0.183	0.126	0.002	-0.053	0.270	0.411	0.262	0.665	-0.021	0.524	-0.112	-0.060	-0.101
MG	0.563	*0.847*	0.646	0.139	0.237	0.573	0.298	0.083	0.238	0.388	0.634	0.231	0.567	0.509	0.635
CL	0.473	0.671	0.230	-0.053	0.369	0.500	-0.050	0.312	0.416	0.521	0.365	0.226	0.582	0.586	0.586
SO4	-0.212	-0.434	-0.456	-0.271	-0.434	-0.458	-0.019	0.144	-0.569	-0.416	-0.592	-0.665	-0.290	-0.255	-0.405
FE	0.075	0.173	-0.192	0.084	0.504	0.277	0.027	0.256	0.600	0.614	0.314	0.563	0.442	0.494	0.448

	TP	MT_24	MT_10D	RAIN_1D	RAIN_15D	LEVEL	NA	CA	K	MG	CL	SO4	FE
TP	1.000												
MT_24	0.680	1.000											
MT_10D	0.733	**0.915**	1.000										
RAIN_1D	0.078	-0.158	0.004	1.000									
RAIN_15D	-0.045	-0.099	-0.044	0.336	1.000								
LEVEL	-0.225	-0.475	-0.366	**0.601**	**0.635**	1.000							
NA	0.833	0.599	0.665	-0.211	-0.102	-0.209	1.000						
CA	0.311	0.408	0.456	-0.202	-0.378	-0.122	0.559	1.000					
K	0.240	-0.111	-0.121	-0.374	0.423	0.152	0.380	0.174	1.000				
MG	0.489	0.578	0.635	-0.256	-0.365	-0.269	0.685	0.903	0.219	1.000			
CL	0.490	0.523	0.484	-0.420	-0.485	-0.166	0.521	0.729	0.069	0.688	1.000		
SO4	-0.426	-0.200	-0.374	-0.117	0.401	0.307	-0.116	-0.307	0.069	-0.373	-0.326	1.000	
FE	0.647	0.243	0.238	-0.234	-0.098	-0.125	0.368	0.408	0.261	0.327	0.682	-0.451	1.000

2.IV Disturbances and invasibility control endemism levels in a freshwater diatom community

Introduction

Disturbance has long been cited as the single most important factor influencing the susceptibility of communities to colonization by introduced species. One consequence of such colonization is the loss of endemic species, which are responsible for a large proportion of global biodiversity and regional distinctiveness, and are an important focus in conservation efforts (Stohlgren et al. 1999, Thomson 2005). There is substantial evidence that introduced plant species do not usually cause loss of native species (including endemics) through direct competition (Levine and D'Antonio 1999, Rosenzweig 2001, but see Sax et al. 2002), but may displace endemics through habitat change and alteration of recolonization patterns following disturbance (Burke and Grime 1996, Davis 2003, Yurkonis and Meiners 2004, McDougall and Turkington 2005).

A rich literature on invasions and their effects exists for macroscopic organisms (see reviews by Parker et al. 1999, Sakai et al. 2001), but the generalizations have rarely been considered in relation to freshwater micro-organisms. Diatoms offer an unusual perspective to the invasions debate because many species appear to have naturally cosmopolitan distributions thus conforming to an established paradigm of ubiquitous dispersal of microbial species <1 mm long (Finlay and Clarke 1999). While most diatoms with cosmopolitan distributions may not be considered invasive in the usual sense (e.g., Rejmanek and Richardson 1996, Kolar and Lodge 2001), they are, by definition, more successful colonizers than more narrowly distributed diatom taxa, suggesting possession of biological and population properties favouring dispersal and establishment.

In a regional-scale analysis, Kilroy et al. (2007 [I]) found that highest proportions of distinctive, regionally endemic freshwater benthic diatoms in New Zealand occurred in communities occupying low-disturbance environments, across a range of productivity levels. In almost all communities these distinctive endemic taxa coexisted with cosmopolitan taxa but coexistence became less prevalent in environments experiencing higher levels of natural physical disturbances, especially where productivity was also high. Thus a connection between physical disturbances and degree of endemism in diatom communities was established on a broad scale, but there was considerable variability in the data. The proportion of endemics in low-disturbance environments ranged from 0 to 100%. This raised questions about how the success of individual species related to both the properties of their environments and the dispersal / colonization capabilities of the organisms. At a local scale (e.g., in a single wetland), overall disturbance and productivity levels may be low, but individual sites (e.g., neighbouring pools) can have very different physico-chemical characteristics (Kilroy et al. in revision [III]), which may be accompanied by contrasting

biological processes. Together these may influence colonisation by and establishment rates of new species.

Recent approaches to understanding species colonisation and coexistence have focussed on properties of the receiving environment rather than on organism properties, emphasising processes that apply to *all* colonizers, both natives and exotics (Huston 2004, Davis et al. 2005). Specifically, increases in resource availability (e.g., from natural climate perturbations, or eutrophication) are expected to increase the chances of successful establishment by a potential colonizer (Huston 2004). The susceptibility of an environment to new colonizers has long been termed "invasibility", with the implication that the diversity of the resident community determines invasibility (e.g., Lonsdale 1999), though the mechanisms for this are controversial (Fridley et al. 2007). However, Davis et al. (2005) proposed that invasibility is an intrinsic, dynamic property of biological communities, determined by disturbance regime, resource use, resource availability, and prior colonization from a regional species pool, and that this property drives diversity. Quantifying invasibility remains difficult, not least because circularity is involved: even though environmental factors contribute to invasibility, species interactions are unavoidably included (Davis et al. 2005). Nevertheless, in the absence of disturbances, it should be possible to combine measures of resources and community characteristics for contrasting sites in the same locality to provide a qualitative assessment of relative invasibility.

In the present study, we investigated the effects of physical disturbances on benthic diatom communities in shallow subalpine mire pools, which have been shown to favour high proportions of endemic diatom species (Kilroy et al. 2007 [I]). Low-level physical disturbances resulting from wind-induced wave action are likely to be the only source of natural disturbance in large, shallow mire pools. We hypothesised that endemic diatoms would be more sensitive than coexisting cosmopolitan species to such disturbances because of differential dispersal and colonisation abilities. To test this hypothesis we assessed the effect of wind-induced wave disturbances on benthic diatom community composition in four pools over two summers. We also generated artificial atypical disturbances, and similarly expected that endemic taxa would be more sensitive than the cosmopolitan taxa.

We then assessed the relative invasibility of the four pools (sensu Davis et al. 2005). We considered the predicted consequences for community characteristics and asked whether our atypical experimental disturbances would affect endemic vs. cosmopolitan population success differently according to the assessed invasibility of the environment. Here, our hypothesis was that endemic species would be most vulnerable to disturbances in the least invasible environments.

In summary, our aims were to determine (i) whether both regular (wind-induced) and atypical (experimental) disturbances in an otherwise stable area impacted endemic diatom species differently from coexisting cosmopolitan species, and (ii) whether differing environmental/biological characteristics, interpreted as a gradient of invasibility, were consistent

with proportions of endemic taxa present initially, and with vulnerability of this endemic component of the community to disturbances. The studied communities included several diatom species identified as endemic to New Zealand (and possibly to a wider biogeographic area encompassing Tasmania). However, a dominant taxon was a species of *Eunophora* (Vyverman et al. 1998), and much of the ensuing discussion relates to this distinctive species.

Methods

Study site

The study area is situated at approximately 1000 m a.s.l., on the northern flank of Bealey Spur near Arthur's Pass, South Island, New Zealand. The 7-ha mire comprises a series of shallow pools of varying size, with substrates comprising soft to firm decomposing organic matter with a surface layer containing live algae, mainly cyanobacteria and diatoms. For further details, including location map, refer to Kilroy et al. (2006, in revision [II, III]). During three years of observations there was no evidence of regular biotic disturbances (e.g., invertebrate or amphibian grazing). The only significant source of regular, natural physical disturbance appeared to be from wind-generated waves in the larger pools. Sampling sites were established on the south-eastern margin of one small pool (pool A), and on the southern margins of three larger pools (B, C and D) (Table IV.1).

Wind-wave effects

A pilot study showed that five samples (pooled) would adequately account for the spatial variability in the common diatom taxa within visually uniform substrate accessible from the pool margin. At approximately fortnightly intervals over the austral summers of 2002/3 and 2003/4, five substrate samples were collected from each of the four pool sites by pushing a 22-mm diameter x 15-mm deep corer into the substrate to enclose a uniform volume of substrate material. Care was taken to minimize disturbance to the area around each sample and samples were taken from pre-designated locations 1–3 m apart, to ensure that each spot was sampled only once (i.e., independence of samples). All samples were collected in a similar water depth (mean of 23 to 29 cm). We also measured a range of physical and chemical variables (Table IV.1) including wave height and water temperature (continuous record, 10-minute intervals) and water column chlorophyll *a*. The latter was extracted in cold acetone after grinding and read fluorometrically at 431 and 670 nm before and after acidification (Downes 1988). We used only data collected in summer (defined as times when mean water temperature over the past 10 days was >12 ºC), when some of the highest wind speeds occurred. Wind had no effect in winter when the pools were frozen, and large temperature variations in spring and autumn were associated with rapid population changes in some diatom species, which would confound separation of wind-wave effects.

Table IV.1. Selected characteristics of the four study pools. In (a) variables, means (with standard deviations in parentheses) are over all summer sampling dates (n = 19) except for benthic chlorophyll *a* (three sampling occasions, n = 12). Different superscript letters indicate significant differences between sites (P < 0.05). (b) Refer to text for explanation of assessment of susceptibility to wind-wave disturbances. n.a. = chips lost in loose substrate but movement assumed to be proportional to fetch as it was at the other three sites.

Pool:	A	B	C	D
(a) Physico-chemical and biological				
Estimated area (m^2)	40	4400	700	1100
Water pH	5.3 (0.21)^a	6.5 (0.22)^b	6.3 (0.18)^c	6.7 (0.27)^d
Dissolved reactive phosphorus (μg/L)	0.26 (0.23)^a	0.53 (0.39)^{ab}	0.30 (0.27)^a	0.67 (0.40)^b
Total dissolved phosphorus (μg/L)	1.6 (0.6)^a	1.3 (0.5)^{ab}	1.1 (0.4)^b	1.7 (0.4)^a
Water column chlorophyll *a* (μg/L)	2.05 (1.7)^a	2.63 (1.42)^{ab}	1.79 (1.2)^a	3.47 (2.35)^b
Benthic chlorophyll *a* (mg/m^2)	133 (55)^a	259 (68)^b	356 (132)^c	155 (53)^a
Number of diatom taxa	14.7 (1.9)^a	14.2 (1.3)^a	9.2 (1.4)^b	20.7 (2.1)^c
Shannon diversity index	2.12 (0.22)^a	1.45 (0.14)^b	0.85 (0.23)^c	2.33 (0.21)^d
% endemics (by biovolume)	50.8 (16.5)^a	90.9 (3.3)^b	92.1(4.4)^b	44.7 (9.0)^a
(b) Susceptibility to wind disturbance (with rank in italics)				
Fetch (m)	3.5 *(4)*	75 *(1)*	25 *(2)*	20 *(3)*
Percentage of coloured chips displaced	0 *(4)*	47% *(1)*	21% *(2)*	n.a. *(3)*
Mean dry wt. suspended following equivalent disturbance (g/L)	1.75 *(1)*	0.82 *(3)*	0.04 *(4)*	1.72 *(1)*
Potential for wind-wave disturbance (order of summed ranks, 1 = most susceptible)	4	1	3	2

Samples were preserved in 2% glutaraldehyde within 4 h of collection, then stored in the dark at <10 ºC prior to taxonomic analysis. The five samples were pooled, homogenized, and made up to a known volume. Measured aliquots were examined under a Leica inverted microscope at 480 ×. At least 400 healthy cells (defined as cells containing intact chloroplasts) were counted from each sample. Cell counts were converted to biovolume per unit area using standard metrics for each species, based on shape and average dimensions taken from at least 15 random cells. To verify species identifications, we made permanent Naphrax®-mounted reference slides of diatoms. Slides were examined at 1000 × using a Leica DMLB microscope. Material was also examined under a Leica S440 scanning electron microscope. Identifications were made using a range of taxonomic texts and each diatom species was assigned either endemic, or non-endemic (likely cosmopolitan) status. Small, rare diatom species that could not be identified with certainty in the preserved

material were omitted from the analysis. These made up 2.4% of the total community, by biovolume, and most were encountered at site D.

An automatic anemometer and windvane (Vector Instruments, Rhyl, UK) were installed at the study area in April 2002. To better reflect wind at the pool surfaces the instruments were placed 1.5 m above ground level, rather than the standard height of 10 m. From the continuous records of wind speed (averaged every 10 minutes), we calculated means and maxima for a range of times up to 12 days prior to each sampling time. The wind record was assumed to be an appropriate measure of water and substrate disturbance for two reasons. First, the two-year record of wind speed and direction showed that almost all high winds in summer were from the same direction (northerly or north-westerly). Fetch (the distance across the water surface) at all sampling sites varied little within each pool over that directional range. Second, wave heights measured at staff gauges showed strong positive correlations with measured wind speeds (e.g., at site B, $R^2 = 0.802$, P = 0.000, $n = 18$, wave height vs. mean wind speed).

To confirm differential wind disturbance at the four sites, we recorded the displacement of fluorescent plastic chips (~2 mm × 3 mm) placed on the surface of the substrate adjacent to the sampling area in each pool. A further factor affecting the potential impact of wind disturbance on the substrate was substrate texture. Loose, flocculent organic material is more liable to be wind-affected than a cohesive mat. To assess this property we created equivalent localized water disturbances in each pool by repeatedly expelling the contents of a turkey baster (tip diameter 5 mm) in the water column at 25 cm above the substrate surface within a 50-mm-diameter length of clear tubing held at the substrate surface then withdrawing 30-ml aliquots of water plus suspended material. Samples from three locations in each pool were filtered onto weighed glass-fibre filters, dried for 24 h and reweighed, for a comparison of material suspended into the water column during these disturbances.

Disturbance experiment

The experiment was undertaken from February to April 2004. In each pool, four areas of uniform substrate were selected and locations within these were randomly designated as treatment (disturbed, two locations) and control (undisturbed, three locations). The design therefore comprised an initial sample from the undisturbed areas ($n = 4$ in each pool), then samples from undisturbed and disturbed locations collected after one and two months ($n = 4$ in each case in each pool). To create an artificial disturbance that did not completely remove species from the disturbed area, a length of clear plastic tubing (50 mm diameter) was gently pushed into the substrate to a depth of about 30 cm. A 80-mm-diameter plastic ring slipped over the tube served as a marker of the disturbed location. The substrate enclosed within the tube was then thoroughly broken up to a depth of about 3 cm by repeated vertical cuts with a metal blade for 1 minute. The disturbed material was allowed to settle back within the tube before removing the tube from the substrate.

Baseline substrate samples (two small cores, pooled) were collected from undisturbed locations in each experimental area, using the method described under "Wind-wave effects" above. After one and two months, we collected samples from one disturbed location and one undisturbed location in each experimental area. Sample treatment, enumeration of diatoms and calculation of biovolumes were as described above. The composition of other algae in the samples was also assessed with quantitative counts of major groups, as follows: colonial unicellular cyanobacteria, dense cells (e.g., *Nostoc*, *Chondrocystis*); colonial, loose cells (e.g., *Aphanocapsa*); cyanobacteria, large single cells (e.g., *Chroococcus*); cyanobacteria, fine trichomes < 5 μm diameter (cf. *Leptolyngbya* spp.); coarse trichomes > 7-15 μm diameter (e.g. *Tolypothrix*, *Hapalosiphon, Fischerella*); desmids; green filamentous algae (e.g., *Oedogonium*, *Mougeotia*); dinoflagellates.

We also measured chlorophyll *a* and phaeophytins in each sample, to determine whether the disturbance affected live algal biomass of the entire algal mat. Chlorophyll *a* and phaeophytin concentrations were determined spectrophotometrically after filtration of a known proportion of the homogenized (unpreserved) sample onto glass-fibre filters, followed by extraction in boiling ethanol (Biggs and Kilroy 2000).[6]

During the course of the study, an opportunity arose to confirm the effects of disturbance at a larger scale, and to track recovery / recolonization of the substrate following a naturally occurring catastrophic disturbance in pool C. In November 2002, a ~3 m x 1.5 m area was severely disturbed by Canada geese (*Branta canadensis*), an introduced species in New Zealand. The cohesive cyanobacterial mat was thoroughly broken up and turned over. Since the disturbed area coincided with part of the designated sampling area, we already had "before disturbance" samples. Subsequently, three replicate samples were taken within the goose-disturbed area approximately fortnightly for three months following the disturbance, with controls from the adjacent undisturbed area. Additional samples (with controls) were taken periodically for up to 6 months, and further samples (at least 3 replicates on successive sampling occasions, 7 – 14 day intervals) at approximately 12, 18 and 24 months after the disturbance. Bird scarers (flags) were installed shortly after the initial disturbance and there was no evidence that the birds re-visited the site.

Data analysis

In all three studies, the benthic community variables of interest were cell biovolumes of combined endemic and combined non-endemic diatom species, and of selected individual taxa, and species richness and diversity (Shannon diversity index = $- \sum i\ p_i \log_e(p_i)$, where p_i is the proportion of the total count for the *i*th species). Biovolumes were expressed as $10^3 \times \mu m^3\ mm^{-2}$ substrate surface area (to a depth of 15 mm). All data were tested for normality and biovolume data were

[6] Note that ethanol and acetone were used to extract chlorophyll *a* from benthic and water column samples (see p. 81), respectively, because the spectrophotometer available was not capable of high enough precision for the water column samples. It is acknowledged that the two methods have differing extraction efficiencies. However, the two measures were not compared with each other.

subsequently log-transformed. For the wind-effects study, correlation analyses for each site showed no covariance between wind speeds and other measured parameters that might influence benthic diatom biomass, including temperature, water column total nutrients, pH and alkalinity. Mean and maximum wind speeds over equivalent periods up to 12 days were highly correlated ($r > 0.89$, $P < 0.001$), and maxima up to 24 h were also highly correlated ($r > 0.75$, $P < 0.01$); we used wind maxima over the previous 3 hours as our main wind variable. Correlations between wind speed and diatom biovolume data (total, endemic, non-endemic and individual species) were quantified using simple linear regression. Wind events were essentially independent of each other (temporal autocorrelation <0.15).

In the small-scale disturbance experiments, additional dependent variables were densities of benthic chlorophyll *a* and phaeophytins (as mg/m^2, to a depth of 15 mm). A two-way ANOVA was used to compare the effects of treatment (controls and disturbed), time, and the interaction of treatment and time at each site. Because of the small size of diatoms (scale of μm) compared to the size of each replicate sampling area (scale of tens of cm), we considered that each sample was spatially independent. The responses of individual variables and species were explored using *t*-tests comparing mean densities in disturbed and undisturbed areas. In these cases, uncorrected P-values are reported because we were interested in the relative numbers and directions of responses in the endemic and non-endemic diatom groups. ANOSIM (PRIMER v. 5) was used to check for significant responses to disturbance in the entire mat community, using percentage biovolumes of major algal groups (including diatoms). For the one-off disturbance in pool C, variables and analyses were as for the small-scale experiment, except that pigment concentrations were not measured. SYSTAT v. 10 was used to carry out all statistical analyses other than ANOSIM.

Assessment of invasibility

Observations during the temporal sampling indicated that wind-waves were the only source of natural disturbance, and the effects were likely to be minor. Therefore we assumed that most biological activity was associated with algal production and respiration. Potential invasibility is partly determined by gradients of resource use and resource availability (Davis et al. 2005). Surrogate measures for these were taken as, respectively: benthic chlorophyll *a*; and water column dissolved reactive phosphorus (DRP), total dissolved P (TDP), chlorophyll *a* and dissolved Si. The N : P ratio in all pools indicated severe P limitation (Kilroy et al., in revision [III]); Si in all pools was typical of that reported in lakes (e.g., Carrick and Lowe 1988). Proportion of the species pool present and species diversity/richness are in general predicted to increase with invasibility (Davis et al. 2005). We determined the former from species counts in an earlier study of multiple pools in the area, in which 81 diatom taxa were distinguished (Kilroy et al. 2006 [II]). The species pool available to each site was calculated taking into account the different pH preferences of species, e.g., pool A (lowest pH) had a smaller species pool than the other three sites.

Results

Diatom taxa

Twenty-two diatom species (Table IV.2) made up most of the diatom community biovolume over all four pools. Nine were considered to have distributions restricted to New Zealand or New Zealand/Tasmania, and are referred to as "endemic" for the remainder of this paper. Across all sites, taxa assessed as endemic made up almost 75% of all cells counted, and ~70% of the biovolume (Table IV.2). Numerically, all four sites were dominated by *Kobayasiella* sp. A, a small, motile, pennate diatom. This species did not conform to any known in the Northern Hemisphere, and most closely resembled *K. acidophila*, described from Tasmania (Vanhoutte et al. 2004). A distinctive taxon similar to *Eunophora oberonica* (Vyverman et al. 1998, and see VI) made up >30% of the biovolume of all cells counted across all sites, and dominated in pools B and C (Table IV.2). Communities at sites B and C contained significantly higher proportions of diatom taxa classified as endemic than sites A and D, but had lower species richness and diversity (Table IV.1).

Wind and wind-wave effects

Mean recorded wind speed from over the summers of 2002–3 to 2003–4 was 2.7 m/s (9.7 km/h), which is equivalent to approx. 18 km/h measured at 10 m above ground level. The maximum recoded wind gust was 13.7 m/s (90 km/h measured at 10 m). Mean and maximum recorded wind speeds of approx. 2 m/s and 5 m/s, respectively, were observed to generate measurable waves on the water surface of pools B, C and D. Fluorescent chip movement confirmed that substrate particles were mobilized in proportion to the fetch at the site (Table IV.1); there was no movement at all in pool A. Substrate consolidation was highest in pool C, and lowest in pools A and D (Table IV.1). From these measures, we predicted that there was highest potential for wind-wave impacts in the largest pool, B, intermediate potential impacts in pool D, minor potential in pool C, and no impacts at all in pool A (Table IV.1).

In pool B, endemic taxa biovolume declined as wind speed increased, showing significant relationships with wind speed (Figure IV.1a). The percentage of the community made up of endemic taxa was also significantly negatively correlated with wind speed ($R^2 = 0.343$, $P = 0.005$, $n = 19$), confirming the pattern in spite of endemic taxa greatly outnumbering non-endemics (Table IV.1(a)). When the biovolume data were separated by year the individual regressions also showed negative relationships with wind speed ($R^2 = 0.492$, $P = 0.004$, and $R^2 = 0.203$, $P = 0.125$). The biovolume of endemic taxa in pool B comprised mainly *Eunophora* cf. *oberonica* and *Kobayasiella* sp. A, both of which declined with increasing wind speed ($R^2 = 0.551$, $P = 0.000$, and $R^2 = 0.304$, $P = 0.009$, respectively). No significant relationships were found in pools A, C or D between wind speed and diatom cell densities or biovolumes (combined endemic or individual species), or at any sites between wind speed and combined taxa assigned non-endemic status, or other individual non-endemic taxa (e.g., Figure IV.1b). Wind speed was also unrelated to water column chlorophyll *a*

Table IV.2. Benthic diatom taxa included in the analysis, with a summary of their responses to disturbances at three scales. Sites where each taxon occurred are listed in order of relative abundance by biovolume. Total abundance (%) is calculated from samples from all four sites over the two summers of the study. Disturbance responses (+ = increase, – = decrease in abundance) are listed for: (a) significant correlations with wind speed (*P < 0.05); (b) differences between disturbed and undisturbed samples (t-tests) for two sampling times; (c) significant difference between disturbed and undisturbed samples in pool C across all sampling times, and on the last sampling occasion. *P < 0.05; ** P < 0.005; # = species not recorded previously appeared in the samples.

Diatom taxa	Pools	Total abund. (%)		Responses to disturbances				
		biovol.	count	(a) Wind	(b) Small scale (blade)		(c) Large-scale (geese)	
Endemic					Mar	Apr	All times	800 days
Eunophora cf. *oberonica*	C, B, A, D	31.3	4.6	–*		–*– *	–**	–**
Kobayasiella sp. A	B, D, C, A	15.6	60.2	–*	–*–		–**	
Amphora berggrenii	B, A, D	10.0	0.6					
Encyonopsis cf. *aequalis*	A	6.5	1.9					
Pinnularia sp. A	D	2.3	0.2					
Kobayasiella sp. B	A	1.7	2.3			–*		
Frustulia sp. A	C, B, D	1.5	1.3				+*	+**
Stenopterobia sp. A	D, B, A, C	0.9	0.4					
Encyonopsis sp. B	D	0.1	1.3					
Non-endemic								
Neidium iridis (Ehrenberg) Cleve	A, D, B	6.6	0.2					
Frustulia saxonica Rabenhorst	D, C, A, B	4.4	0.6			–*	–*	
Stenopterobia curvula (W. Smith) Krammer	D, B	2.7	0.3				#	
Pinnularia macilenta Ehrenberg	A, B	2.4	0.2				#	
Stenopterobia delicatissima (Lewis) Van Heurck	A, D	2.1	1.1				+* #	+**
Encyonema neogracile Krammer	D, B, C	1.9	2.3			+*		+**
Eunotia bilunaris var. *mucophila* Lange-Bertalot & Norpel	A., B, C	1.9	7.6					
Brachysira wygaschii Lange-Bertalot	A, D, B, C	1.8	0.4			+*	+*	+**
Brachysira brebissonii Ross ssp. *brebissonii*	A, D, B, C	1.6	3.2				+*	+**
Tabellaria flocculosa Roth	D, B, C	1.1	1.1					+*
Pinnularia biceps Gregory	D, A, B	0.8	0.1				#	
Brachysira microcephala (Grunow) Compère	D	0.3	1.3					
Kobayasiella parasubtilissima (Kobayasi & Nagumo) Lange-Bertalot	B, D, C, A	0.1	1.9		+*	+* +*		

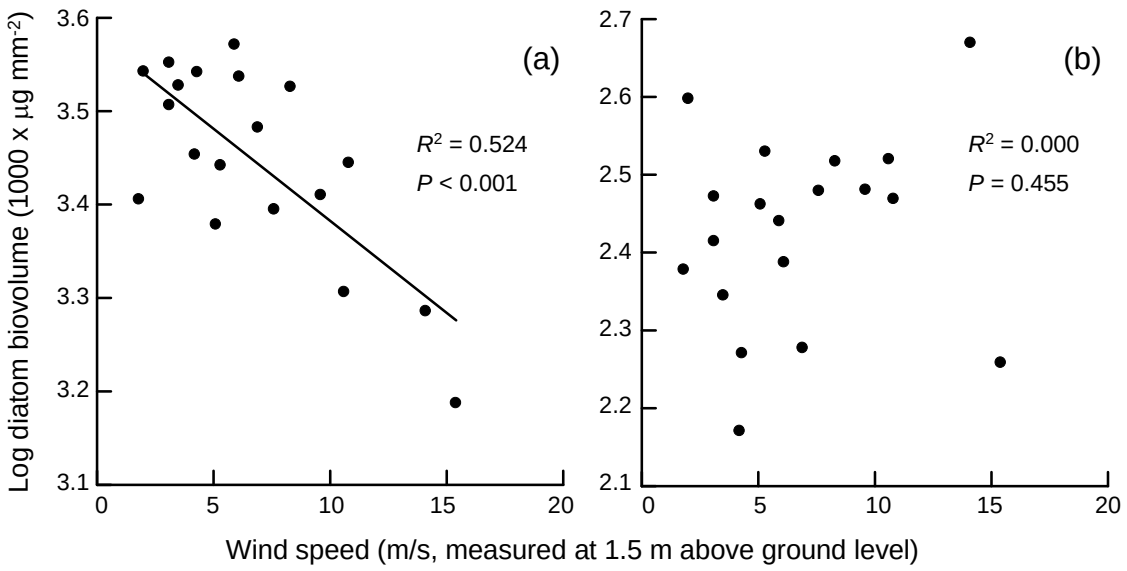


Figure IV.1. Relationships between wind speed and densities of (a) endemic and (b) non-endemic benthic diatoms in pool B, over two summers (2002/3 and 2003/4) combined.

(pool B, $R^2 = 0.000$, P = 0.335), suggesting that the decline in benthic diatoms was not simply because live cells were temporarily being suspended into the water column.

Disturbance experiment

Site markers were lost in the soft substrate of pool D, therefore only partial data are available, and complete results are presented for pools A, B and C only. The three sites showed a gradient of responses to small-scale disturbances (Figure IV.2, Table IV.3). In pool A, there were no significant differences between disturbed and undisturbed areas after 2 months (Figure IV.2a-f, Table IV.3), although species richness, diversity, chlorophyll *a* and phaeophytin showed responses after 1 month (Figure IV.2c-f). In pool B endemic diatom biovolume and chlorophyll *a* declined in the disturbed areas, while phaeophytin density rose (Figure IV.3g, k, l). In pool C, endemic taxa biovolume declined, while species richness and diversity increased in the disturbed areas (Figure IV.2m, o, p). The only variable that did not change at any site with respect to disturbance was the biovolume of non-endemic diatom taxa (Figure IV.2b, h, n; Table IV.3). One set of samples ($n = 4$) from pool D after 1 month (March) showed no effects of the disturbance after one month in all variables except for a significant rise in phaeophytins ($P < 0.05$, data not shown).

Diatoms comprised between ~15 and ~45% of the total algal community in the four pools. Cyanobacteria made up around 50% of the community in all pools, but the composition of this component varied (Figure IV.3a). Pools A and D contained more chlorophytes (mainly *Oedogonium* sp.) than pools B and C, and we found significant numbers of dinoflagellates only in pool C. Community composition in all pools significantly differed from all others (ANOSIM $R = 0.281$, $P < 0.05$). There was no significant response to disturbance in the overall mat communities

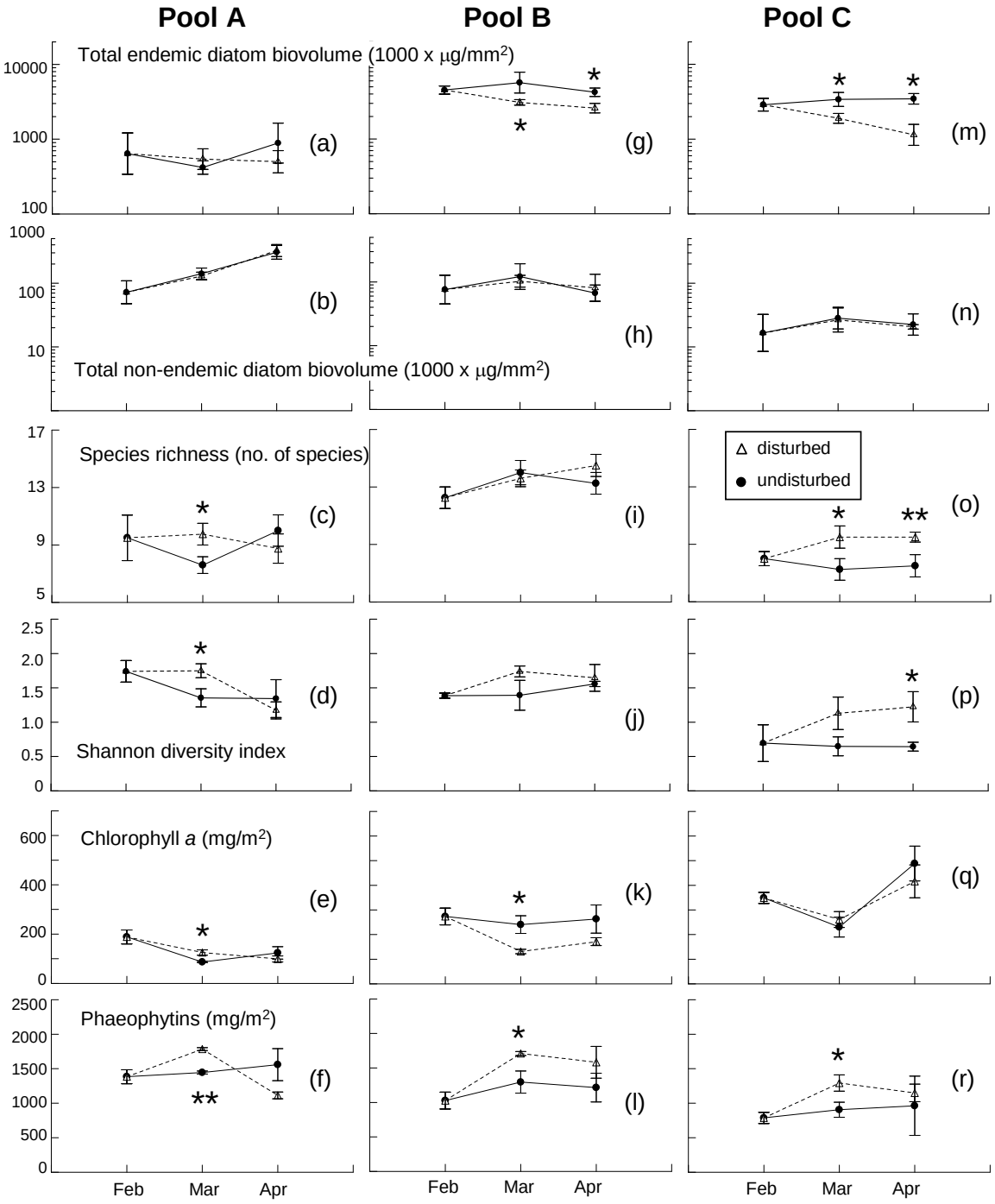


Figure IV.2 Small-scale disturbance experiment. Changes in benthic diatom densities (endemic and non-endemic groups), species richness, Shannon diversity, and algal pigment concentrations in experimentally disturbed (dashed lines) and undisturbed areas (solid lines) of three pools, over two months. Error bars indicate ± 1 SE. Significant differences (uncorrected) between disturbed and undisturbed areas are indicated by * ($P < 0.05$) or ** ($P < 0.005$) (t-tests, $n = 4$).

Table IV.3. Results of 2-factor (Time = 0, 1 month, 2 months, Disturbance = disturbed or undisturbed) ANOVA examining the effect of small-scale disturbances over time in three pools at Bealey Spur wetland, on a range of community indices. *F* values are followed by probabilities, with significant values (P < 0.05) in bold type.

Pool	Variable	Disturbance	Time	Disturbance x Time interaction
A	log total biovolume (endemic)	0.150 (0.703)	0.395 (0.679)	0.562 (0.579)
	log total biovolume (non-endemic)	0.424 (0.523)	17.313 (**0.000**)	0.040 (0.961)
	Species richness	0.119 (0.734)	0.455 (0.641)	1.688 (0.211)
	Shannon diversity	0.228 (0.639)	5.891 (**0.010**)	2.236 (0.134)
	Chlorophyll *a*	0.119 (0.734)	15.701 (**0.000**)	1.923 (0.174)
	Phaeophytins	0.228 (0.639)	5.520 (**0.013**)	9.459 (**0.001**)
B	log total biovolume (endemic)	10.248 (**0.005**)	3.324 (0.058)	2.605 (0.100)
	log total biovolume (non-endemic)	0.001 (0.970)	0.947 (0.406)	0.106 (0.900)
	Species richness	0.311 (0.584)	4.265 (**0.030**)	0.956 (0.402)
	Shannon diversity	2.935 (0.103)	2.398 (0.118)	1.549 (0.238)
	Chlorophyll a	8.760 (**0.008**)	5.140 (**0.016**)	2.214 (0.137)
	Phaeophytins	6.197 (**0.022**)	7.569 (**0.004**)	1.552 (0.237)
C	log total biovolume (endemic)	14.557 (**0.001**)	2.161 (0.144)	4.557 (**0.025**)
	log total biovolume (non-endemic)	0.013 (0.912)	0.758 (0.483)	0.005 (0.995)
	Species richness	10.975 (**0.004**)	0.494 (0.618)	2.772 (0.089)
	Shannon diversity	5.937 (**0.025**)	1.010 (0.384)	1.623 (0.245)
	Chlorophyll a	0.188 (0.669)	13.934 (**0.000**)	0.920 (0.995)
	Phaeophytins	1.965 (0.178)	2.049 (0.158)	0.672 (0.523)

in pools A. B and D, but a significant change in pool C (ANOSIM $R = 0.326$, P = 0.002). The averaged data showed that the proportion of diatoms declined noticeably following the disturbance in pool C, and proportions of several other groups increased, in particular dinoflagellates (Figure IV.3a,b).

The negative response by endemic diatom taxa to the small-scale disturbance in pool C was confirmed by the community response to the Canada goose disturbance in pool C. Total diatom biovolume declined markedly immediately following the disturbance event, mainly as a result of a tenfold decrease in the biovolume of *Eunophora* cf. *oberonica* and an approximately 90% reduction in the biovolume of *Kobayasiella* sp. A (Figure IV.4a,d,e). The latter recovered to non-disturbed biovolumes by 400 days, but *E.* cf. *oberonica* levels remained depressed until the

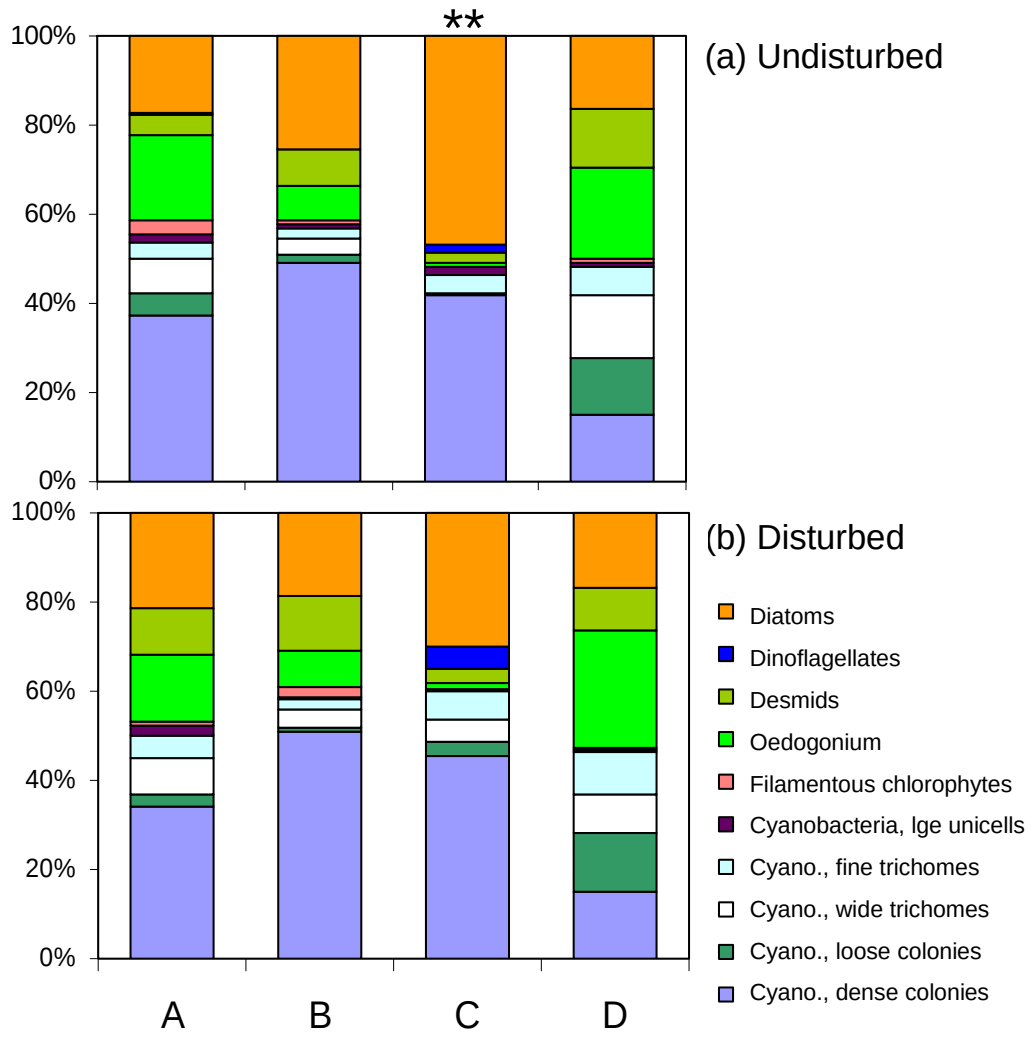


Figure IV.3. Mean relative abundances of major algal groups in the four pools in (a) undisturbed and (b) disturbed areas in the small-scale disturbance experiment (*n* = 4). **indicates a significant difference in community composition following disturbance (ANOSIM, P = 0.002). All sites differed from all others (ANOSIM, P < 0.005). (Refer to p. 84 for more information on the taxa in each algal group.)

end of the monitoring period. Conversely, the endemic *Frustulia* sp. A increased in density in the disturbed area, and subsequently remained significantly higher than in the control samples (Figure IV.4f). The biovolume of combined non-endemic diatoms in the disturbed area remained similar to that in the undisturbed area (Figure IV.4c). Responses of individual non-endemic species varied (Figure IV.4g-k). Diversity rose significantly following disturbance, and stayed higher throughout the study, presumably partly due to the decline in dominance by *E.* cf. *oberonica*, but also due to the appearance in the samples of additional species that had not previously been recorded in pool C (Table IV.2). ANOVA results are presented in Table IV.4. Note that in many cases the differences between disturbed and undisturbed communities were accompanied by changes through time, which are expected in natural communities of micro-organisms.

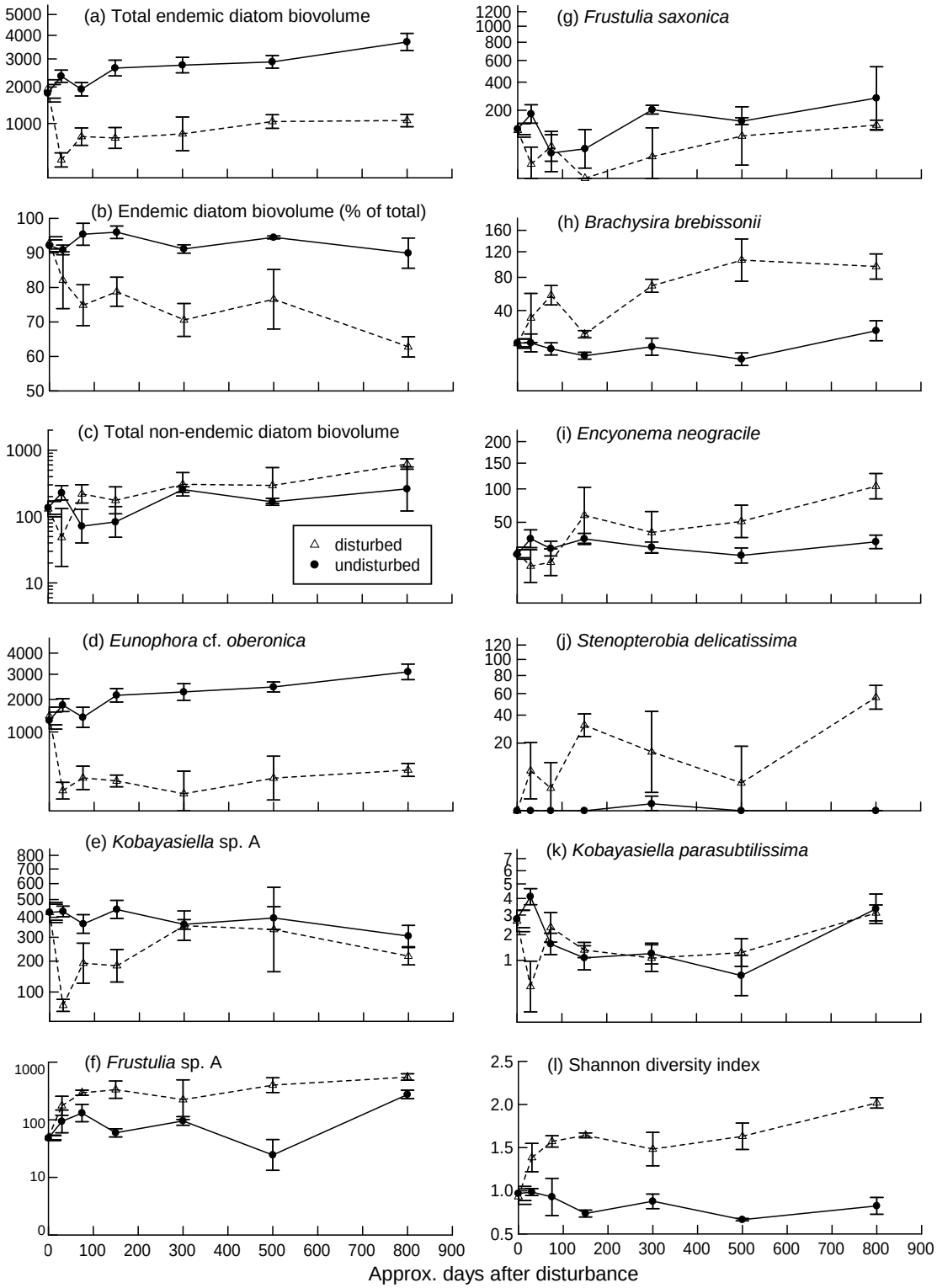


Figure IV.4. Changes in diatoms densities (endemic and non-endemic groups and individual species) and species diversity for two years following substrate disturbance by Canada geese in pool C. Dashed lines show responses in disturbed areas; solid lines are samples from adjacent undisturbed areas. (d) – (f) are endemic species; (g) – (k) are non-endemics. Biovolumes in (a) – (k) are in 1000 x $\mu m^3/mm^2$. Error bars indicate ± 1 SE.

Table IV.4. Results of 2-factor (Time = 0, 90, 200, 400, 550 and 800 days, Disturbance = disturbed or undisturbed) ANOVA examining the effect of analysis of variance of the effect of a larger-scale disturbance at site C, Bealey Spur wetland, on a range of community indices and individual diatom taxa. F values are followed by probabilities, with significant values (P < 0.05) in bold type.

Variable	Disturbance	Time	Disturbance x Time interaction
log total biovolume (endemic taxa)	39.122 (**0.000**)	7.656 (**0.000**)	1.103 (**0.000**)
log total biovolume (non-endemic taxa)	0.166 (0.685)	16.813 (**0.000**)	3.174 (0.080)
Shannon diversity	23.627 (**0.000**)	13.701 (**0.000**)	36.339 (**0.000**)
% endemic taxa (by biovolume)	13.141 (**0.000**)	19.928 (**0.000**)	13.616 (**0.000**)
Endemic species			
Eunophora oberonica	20.241 (**0.000**)	0.331 (0.567)	0.559 (0.458)
Kobayasiella sp. A	20.485 (**0.000**)	0.053 (0.0.819)	2.407 (0.126)
Frustulia sp. A	6.904 (**0.011**)	10.885 (**0.002**)	1.570 (0.215)
Non-endemic species			
Frustulia saxonica	8.191 (**0.006**)	3.959 (0.051)	0.871 (0.354)
Brachysira brebissonii	12.110 (**0.001**)	14.298 (**0.000**)	7.662 (**0.007**)
Encyonema neogracile	3.591 (0.063)	15.015 (**0.000**)	13.589 (**0.000**)
Stenopterobia delicatissima	6.164 (**0.016**)	12.517 (**0.001**)	12.077 (**0.001**)
Kobayasiella parasubtilissima	1.868 (0.177)	0.554 (0.459)	1.999 (0.162)

Overall, species-specific responses in the small and larger scale disturbance studies showed declines in endemic taxa and increases in the non-endemics following disturbance, though there were exceptions (Table IV.2).

Assessment of relative invasibility

Invasibility was assumed to be positively correlated with nutrient availability (DRP, TDP, water column chlorophyll *a* and Si) and negatively with resource usage (benthic chlorophyll *a*). The summed ranks of these variables gave an initial assessment from least to most invasible of pools C, B, A, and D (Table IV.5). The order of % of species pool, species richness and Shannon diversity conformed to predictions of a positive correlation with invasibility in the absence of disturbances (Davis et al. 2005) (Table IV.5).

Table IV.5. Assessment of relative invasibility of the four study sites, and ranks of diatom community measures predicted to be determined by invasibility. Resource availability and resource usage were determined from, respectively, mean water column DRP and TDP, and mean benthic chlorophyll *a*. % of species pool was determined from species counts in an earlier study of multiple pools in the area, in which 81 diatom taxa were distinguished (Kilroy et al. 2006 [paper II]). For all variables, mean values are shown in parentheses.

	Pool			
	A	**B**	**C**	**D**
1. Assessment of invasibility (ranks, 1 = favours high invasibility)				
Resource availability				
water column DRP, μg/L	3 (0.3)	2 (0.5)	3 (0.3)	1 (0.7)
water column TDP, μg/L	1 (1.6)	3 (1.3)	4 (1.1)	1 (1.7)
water column chlorophyll *a* (μg/L)	3 (2.05)	2 (2.63)	3 (1.79)	1 (3.47)
water column dissolved Si, mg/L	1 (0.43)	3 (0.31)	3 (0.31)	1 (0.41)
Resource usage				
benthic chlorophyll *a*, μg/L	1 (133)	3 (259)	4 (356)	1 (155)
Invasibility rank (order of summed ranks in above lines)	**2**	**3**	**4**	**1**
2. Predicted outcomes of invasibility				
% species pool	2 (36)	3 (30)	4 (18)	1 (41)
Species richness	2 (14.7)	2 (14.2)	4 (9.2)	1 (20.7)
Diversity (Shannon index)	2 (2.12)	3 (1.45)	4 (0.85)	1 (2.33)
% endemic taxa	1 (50.8)	3 (90.9)	3 (92.1)	1 (44.7)

Discussion

In this study we examined the responses of benthic diatoms assessed as endemic and non-endemic to disturbances of different intensities within an environment characterized by low natural levels of disturbance. Our first hypothesis – that endemic species are expected to be more sensitive than coexisting cosmopolitan taxa to wind-wave and experimental disturbances in an otherwise stable environment – was supported for the dominant endemic taxa. First, in pool B, which was predicted to be most impacted by wind-wave disturbance, both *Eunophora* sp. and *Kobayasiella* sp. A (which made up most of the endemic group) declined in abundance as wind speeds increased, while non-endemic taxa were unchanged, suggesting differential sensitivity to suspension into the water

column. However, since the total populations of these species within the substrate were so high compared to the declines, the overall effects would be expected to be minor and short-lived. Second, the small-scale, but more intense, disturbances also showed negative impacts on the endemic diatom group in the medium term (up to 2 months) in pools B and C. Following the larger disturbance by Canada geese in pool C, negative impacts on endemic taxa, especially *Eunophora* cf. *oberonica*, were intensified and prolonged while effects on the non-endemic group were non-significant. Therefore, the importance of habitat stability in maintaining populations of at least some endemic diatom taxa was supported in the study area.

Our assessment of the relative invasibility of the four sites (i.e., C, B, A and D, from lowest to highest) was paralleled by higher levels of endemism in pools C and B (92% and 91% by biovolume, respectively) than in pools A and D (51% and 45% by biovolume, respectively). As hypothesised, ranked invasibility also matched the gradient of response to the small-scale disturbances, with pool C most strongly affected, followed by pool B, and no significant effects in pool A or D (the latter inferred from partial data).

A prerequisite to the link between invasibility and endemism levels is likely to be historical stability at a site: as soon as an atypical disturbance occurs, invasibility increases (Davis et al. 2005, and see below). In the case of the Bealey wetland, stability equates to extremely low levels of background (wind-wave) disturbance. This is achieved to the extreme in pool C in which the consolidated substrate apparently resists wind-induced disturbances. These mats (and to a lesser extent, the increasingly less consolidated mats in pools B, A and D) showed the stratified structure typical of cyanobacterial mats from other locations (e.g., Wiggli et al. 1999, Villeneuve et al. 2001, Sabbe et al. 2004). An upper orange-brown layer (~2 mm thick) overlaid a green layer, with darker material at the base. Nutrient and dissolved ion concentrations are typically much higher within such cyanobacterial mats than in the overlying pool waters (e.g., Vincent et al. 1993, Villeneuve et al. 2001). High within-mat nutrient concentrations suggest internal recycling of nutrients creating a favourable habitat for resident algae. Therefore the mechanism for the effect of an atypical disturbance, such as our small-scale experiment, could simply have been disruption of the habitat structure and accompanying favourable conditions for *Eunophora* cf. *oberonica* and *Kobayasiella* sp. A, leading to population declines in these diatoms. In this situation, disturbances could also cause nutrients to be released into the surrounding surface water, increasing the chances that arriving species will not be nutrient-limited. For pool C this is consistent with increasing proportions of other algal groups following the small-scale disturbance (Figure IV.3). In pool C, the very long recovery time following the goose disturbance again may have had more to do with destruction of the specialised habitat required by *Eunophora* cf. *oberonica* than poor colonisation capability in this species. However, it was notable that diatom species not previously found in pool C were recorded in the disturbed area for the first time, and all of these were assessed as non-endemic (Table IV.2).

Although we made no detailed measurements of pore-water chemistry during the present study, within-mat and water column differences were confirmed qualitatively. We measured dissolved nutrient concentrations in subsurface waters by allowing distilled water sealed in dialysis tubing to equilibrate within the mats for two weeks. Average concentrations (n = 3 – 6) were 2 (DRP in pool B) to 29 (NH_4 in pool C) times higher than in the overlying waters and the ratios tended to be highest in pool C (C. Kilroy, unpublished data).

While decoupling can occur between some processes in the water column and benthos of lakes in general (Lowe 1996), stronger links have been reported (e.g., Blumenshine et al. 1997). In pools A and D, the less consolidated substrates appear to provide a closer link between conditions in the mat and in the water column than the firm mats in pools B and C (see Paper VI). This is consistent with the lack of response in pools A and D (partial data for pool D) to the small-scale disturbances, particularly at the time scale (one month) over which we collected samples. The disturbances may have had a shorter-term impact (and this is suggested by declines after 1 month for species richness, diversity and phaeophytins in pool A). However, the loose substrate offers little resistance to disturbances and is predicted to be relatively resilient to physical disruption because cells would experience little change in, or possibly enhanced, conditions when temporarily removed into the water column (Peterson 1996).

Overall then, the four pools in the present study represented a gradient in water-column – benthos linkages, which are paralleled by a gradient that can be interpreted as invasibility with respect to the benthic diatom community. In other words, in the present example, the key to differential invasibility and responses of diatoms to atypical disturbances in the four pools may lie in linkage between the substrate and the overlying waters, which itself is linked to the degree of consolidation of the substrate. Species diversity followed the same gradient and this is consistent with low invasibility leading to low species diversity (Davis et al. 2005) when a few taxa (either native or exotic) are able to sequester available resources or change microhabitat conditions such that potential new colonists are often unsuccessful (e.g., Yurkonis and Meiners 2004).

This habitat-specific explanation of the different responses to disturbance in the four pools can be transferred to more general theory. Disturbances can lead to either increases or decreases in diversity, depending on the effect on resource supplies or interactions with other species (Huston 2004). Recent studies suggest that species interactions (e.g., competition) are not as critical as has been traditionally assumed in facilitiating dominance of exotic species (Levine 2000, MacDougall and Turkington 2005). If an environment already has under-used resources then it follows that a physical disturbance that changes that resource base in either direction may not affect the resident species provided that no structural changes to microhabitats occur. In the present case, it seems that the structural change in more consolidated cyanobacterial mats both disrupts habitat and could release nutrients for colonising species.

The environmental processes that have resulted in such a strong gradient of substrate types within close proximity in the same mire system are unclear, and likely relate to the development of the mire system over time (Foster and Fritz 1987). At the same time, the pools themselves have clear differences in water chemistry that can be attributed to both hydrology and pool size (Kilroy et al. in revision [III]). Presumably the differences in algal composition of the substrate observed among the pools (Figure IV.3) are maintained by these physico-chemical differences. For example, different pH and alkalinity regimes would favour different types of algae.

In analysing our data, we considered endemic and non-endemic species as single groups with potentially different properties. Thus, all taxa known to have wide distributions would show superior recolonization capabilities compared with all taxa with more restricted (endemic) distributions. As discussed above, *Eunophora* cf. *oberonica* was responsible for most of the response in the endemic group, with one other endemic species (notably *Kobayasiella sp. A.*) also responding as hypothesized (Table IV.2). The endemic *Frustulia* sp. A, on the other hand, sometimes showed a positive response to disturbance (Table IV.2). The contrasting responses of *E.* cf. *oberonica* and *Frustulia* sp. A may be explained with reference to their biology. Observations on live material during the present study indicated that *E.* cf. *oberonica* is not highly motile, and lives closely associated with cyanobacterial colonies and fine trichomes. *Frustulia* sp. A, like other species in this genus, appeared to be highly motile. Motility has been shown to be a photo-sensitive reaction that enables species to optimize their light environment, e.g., in soft sediments (Cohn and Weitzell 1996), thereby possibly conferring an advantage to some species following substrate-disrupting disturbances. In contrast, we observed that the endemic *Kobayasiella* sp. A appears to be highly motile, yet displayed a negative response to disturbances in pools B and C, but not in pools A and D. This may relate to larger micro-environmental changes following disruption of consolidated mats compared with the loose substrate, but further studies would be needed to determine the exact causes.

Growth rates may also determine responses to disturbances, as seen in more rapid recolonization by small species capable of rapid cell division (Peterson and Hoagland 1990). A negative relationship between diatom cell size and cell division rates has been noted in several studies (Mizuno 1991), thus we would expect smaller species (e.g. *Kobayasiella* sp. A, *Frustulia* sp. A) to recover and recolonize faster than larger species (*E.* cf. *oberonica*). The cosmopolitan species that responded positively or showed no response to the small-scale disturbances and / or the larger scale disturbance in pool C (*Brachysira brebissonii*, *Stenopterobia delicatissima*, *Encyonema neogracile* and *K. parasubtilissima*) were all relatively small, motile species. All have been reported from similar habitats worldwide. A single non-endemic species (*Frustulia saxonica*) responded negatively to both disturbances (Table IV.2), but appeared to recover from the larger goose disturbance (Figure IV.4g). *F. saxonica* is a relatively large, motile species that has a reported cosmopolitan distribution (VI).

In summary, these studies have shown in a naturally stable environment that some benthic diatoms classified as endemic are more susceptible to disturbances than co-existing non-endemic species. *Eunophora* cf. *oberonica* and possibly *Kobayasiella* sp. A appear to have specialised environmental requirements that make them especially sensitive. Despite recent assertions that diatom species are, as a rule, globally dispersed (Finlay et al. 2002), we find that some species with evidently narrow geographical distributions (i.e., endemics) can be vulnerable to disturbances in the same way as endemic plants (e.g., Thomson 2005). At the same time, other species assessed as endemic showed either no response or a positive response to disturbances. In this study, no non-endemic species displayed invasive behaviour in this environment through, for example, very rapid population growth (Rejmanek and Richardson 1996). Given the low overall productivity of these mire pools (Kilroy et al. in revision [III]), this is consistent with low *absolute* invasibility of such environments (Huston 2004). However, some diatom species do have invasive traits, notoriously *Didymosphenia geminata* (Kilroy 2004). Therefore benthic diatom communities inhabiting naturally stable environments with extremely low invasibility (such as pools B and C) are likely to be particularly vulnerable to either increases in nutrient levels or intensification of disturbance events.

2.V Coexistence of endemic and non-endemic benthic diatoms: the roles of scale, community dynamics, and environmental interactions

Introduction

All biological communities comprise interacting species whose population sizes vary spatially and temporally as a result of environmental and biological processes. Species coexistence (and therefore maintenance of biodiversity) has traditionally been explained by a combination of competitive interactions, environmental fluctuations, resource partitioning (spatial and temporal), disturbances, and immigration from a species pool (Huston and DeAngelis 1994, Zobel 1997, Chesson 2000). More recently, neutral theory has been proposed, in which all species are considered competitively equivalent and community composition at any time is determined by random immigration and population size (e.g., Chave 2004). Central to this theory is the concept of the metapopulation: the spatially large background of interconnected communities of multiple species within which local community dynamics occurs (Leibold et al. 2004).

Much of the literature on species coexistence patterns concerns macro-organisms and increasingly, both theoretical and experimental studies have focussed on the universal occurrence of non-indigenous species (NIS) and their possible effects on native, including endemic, species (Rosenweig 2001). Microorganisms may be fundamentally different in that many taxa are thought to have naturally cosmopolitan distributions (Finlay 2002), such that microbial NIS or endemic species cannot exist. While there is little doubt that some microbial species are truly cosmopolitan, there is also increasing evidence of local and regional endemism in microorganisms (e.g., see reviews by Foissner 2006, Vyverman et al. 2007a). Additionally, some recent analyses have shown that in some respects metapopulation patterns in diatoms do not differ greatly from those in macroscopic organisms (Soininen and Heino 2005, Vyverman et al. 2007b), but others have shown differences that can be attributed to high dispersal abilities (Hillebrand et al. 2001).

In New Zealand freshwaters, distribution patterns of distinctive, assumed endemic, benthic diatom species broadly conform to those observed for macroscopic organisms (Kilroy et al. 2007 [I]). Many of the diatom species assessed as endemic or very likely to be endemic occurred in low disturbance, low productivity habitats. These included in particular high-altitude mire pools and tarns – habitats where the diatom flora was previously poorly known. Within these habitats, the endemic species usually coexisted with cosmopolitan taxa in the same community. This raised the question of how the endemics persisted, assuming that diatoms with cosmopolitan distributions may be analogous to NIS or invasive species.

For macro-organisms, in spite of a perception that NIS are “bad” (Fritts and Rodda 1998), a common finding is that direct interspecific competition is not responsible for the decline of native species, and declines usually result from other processes such as habitat alteration or habitat destruction (Gurevitch and Padilla 2004, Thomson 2005). However, the impacts of invaders on native communities have shown contrasting results depending on scale. Thus, at scales of 10 m^2 or less, resistance to invasions appears to be positively correlated with species richness (i.e., species-rich communities, usually experimental, are less likely to be invaded), whereas at larger scales, species-rich, natural communities appear more likely to be invaded. This is the so-called “invasion paradox” (e.g., Davies et al. 2005; Fridley et al. 2007), although a similar pattern can be generated by neutral models (Fridley et al. 2004, Herben et al. 2004). Superimposed on species changes are properties of the environment, including productivity, disturbances and spatial and temporal variability, all of which can influence susceptibility to invasion at any given time and have received considerable theoretical and empirical attention (e.g., Chesson 2000, Davis et al. 2005, Snyder 2007). It is now thought that colonization of a community by a NIS is likely to be no different from colonization by a previously absent native species (Burke and Grime 1996, Davis et al. 2005) and that invasion and coexistence theories are essentially congruent (Melbourne et al. 2007). In terms of microorganisms – specifically freshwater diatoms – this implies that coexisting endemic and cosmopolitan species should show community patterns expected in other, larger, organisms.

In the present study, we investigated whether coexisting endemic and cosmopolitan benthic diatom species differ in their abundance patterns, and whether the patterns are comparable to those observed for larger organisms. Subsequently in this paper, species known not to be confined to New Zealand, or the biogeographic region encompassing Tasmania (Kilroy et al. 2007 [I]) are referred to as “non-endemic” to account for uncertainty in the range sizes of some taxa. We present data on the occurrence of endemic and non-endemic diatom taxa in a uniform habitat type, subalpine mire pools. Mire pools provide a suitable model system for a metacommunity study (Leibold et al. 2004) as they are analogous to islands in a larger connected landscape. The microbial community at sites within a pool is likely to comprise interacting individuals and populations, and these communities will be open to immigration from other pools, depending on their distance from each other. Further, the diatom communities of mire pools tend to be restricted to a suite of acidophilous genera (e.g., Kilroy et al. 2006 [II]). Therefore, immigration will generally be from similar habitats. Our data covered three different scales: the South Island of New Zealand, multiple pools in a single mire system, and four individual neighbouring pools over a two-year period.

Using the three datasets, we addressed a hierarchy of questions (Figure 1):

1. Do the abundance–occupancy relationships for benthic diatoms in mire pools conform to those observed for macroscopic organisms (Gaston et al. 2000) and for other diatom communities

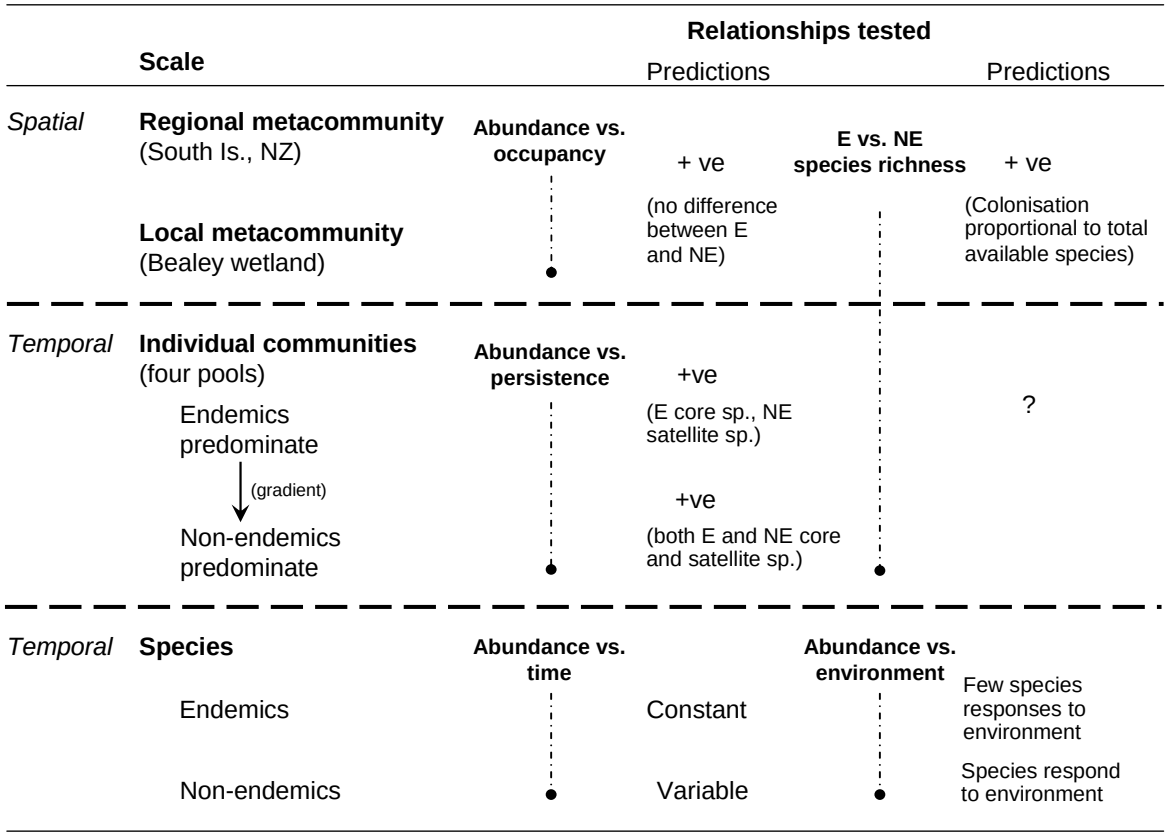


Figure V.1. Summary of relationships to be tested in an investigation into the coexistence of endemic and non-endemic benthic diatoms in mire pools, using three datasets of diatom community composition covering different scales. Vertical lines indicate repeats of the relationships over different scales or gradients. Included under "Predictions" is the direction of the relationship observed in macro-organisms (+ve, or a "?" if unknown), with comments in parentheses regarding expected conformity to these patterns in the present data. Refer to text for details. E = endemic species; NE = non-endemic species.

(Soininen and Heino 2005)? A positive interspecific abundance–occupancy relationship "may be one of the most general patterns in ecology" (Gaston et al. 2000). No single explanation has been identified for the relationship, and most of the proposed mechanisms appear likely to operate independently of an organism's overall range size. Therefore we would expect the relationship for these diatom communities to be similar to that in macro-organisms.

2. Are abundance–persistence patterns for benthic diatoms in mire pools consistent with those observed in macro-organisms, i.e., similar to spatial patterns (Magurran 2007)? Compared to spatial patterns of species abundance (Gaston et al. 2000, Hillebrand et al. 2001), the related – and remarkably similar – temporal patterns have been relatively neglected; yet knowledge of temporal patterns may be crucial for understanding how rare (including endemic) species persist (Magurran 2007). Soininen and Heino (2005) showed that these parallel temporal patterns are also seen in stream diatom communities, therefore we expected similar results with the present data.

3. Do endemic species in these environments show similar abundance–occupancy and abundance–persistence relationships as the non-endemic species? Our hypothesis here was that we would not expect differences at the metacommunity scales, except that in a world of ubiquitous diatoms (Finlay et al. 2002) most endemic species should be uncommon. However, at the scale of a single community, endemic and non-endemic species could show different patterns, depending on habitat characteristics. Theory suggests that locally dispersing species accumulate in favourable habitats (the "spatial storage effect", Chesson 2000). Thus, at some sites, endemic species, with restricted dispersal capabilities, might be expected to predominate as "core" species (i.e., species occupying sites continuously, as opposed to "satellite" species, which occur sporadically, Hanski 1982) if conditions are especially suitable.

4. Is endemic diatom species richness related to non-endemic species richness in the same community? In other words is there any tendency for an endemic species to coexist with other endemics rather than other non-endemics? Endemism in some groups of macroscopic organisms is positively related to the number of species in the community with wider distributions (Vilenkin and Chikatunov 2000, Fattorini 2007). There may also be an analogy in endemic and non-endemic diatoms with the commonly found pattern of a positive relationship between exotic and native species diversity at larger spatial scales (e.g., Davies et al 2005, Fridley et al. 2007).

Using the third (temporal) dataset only, we then looked in more detail at the population dynamics of benthic diatom taxa at four sites. Glazier (1986) observed that, in some groups of macro-organisms, geographic range size is positively correlated with the extent of temporal fluctuations in local populations. The proposed mechanism was that species with small ranges tend to be habitat specialists. Such organisms would tend to go extinct rapidly if they experienced wide abundance fluctuations. In contrast, species with larger range sizes (i.e., superior dispersal capabilities) may have more opportunistic life histories, enabling them to repeatedly colonise unstable habitats. If this holds for diatoms, we expect that the effect would be evident only for the core species in a community (Hanski 1982) because variability is high in satellite (i.e., rare) species by definition. Glazier's 20-year-old observation has apparently featured rarely in subsequent literature, but in the present case seems relevant in explaining the presence of small-scale centres of endemism in diatoms in environmentally variable landscapes.

Environmental variability (both spatial and temporal) has been shown to be critical for the maintenance of species diversity and the success of invasions (Davies et al. 2005, McCabe and Cyr 2006, Melbourne et al. 2007). Therefore we also considered the environmental characteristics of each site in relation to the population and community variability, again hypothesizing that non-endemic taxa would be more likely to respond to environmental (including seasonal) changes (Glazier 1986).

In summary, the overall aim of this work was to describe and explain the coexistence of endemic benthic diatom species (by definition, poor dispersers) with coexisting non-endemic taxa (by definition successful dispersers and colonizers) in terms of general ecological patterns observed in macro-organisms. Given the prevailing view that coexistence and invasion are synonymous in larger organisms (Davis et al. 2001, Melbourne et al. 2007) we did not expect differences between endemics and non-endemics at the scale of metacommunities. Any differences should be evident only at species population level in individual communities.

Methods

South Island data set

The data comprised diatom relative abundances assessed on samples from 69 subalpine mire pool sites throughout the South Island, New Zealand. All samples were collected between 1999 and 2004 using standardised collecting methods (Kilroy et al. 2007 [I]). Permanent slides of diatom samples were prepared using standard methods (Biggs and Kilroy 2000) and examined microscopically at 1000x. A visual assessment was made of the relative abundance by biovolume of each taxon on a scale from 1 (rare) to 8 (dominant) using the method described in Biggs and Kilroy (2000). Consistent effort was applied to each slide. Species identifications were made using a range of literature (see Kilroy et al. 2007 [I]). All species were assigned either to a non-endemic group (i.e., indistinguishable from species described and recorded from regions other than the New Zealand–Tasmania–E. Australia region), or an endemic group (known only from this region, or suspected new species from this region) using published distribution information, or species-specific studies (VI). Approximately 10% of the 180 species distinguished could not be assigned to either group because of lack of information. However, almost all of these occurred at only one site and therefore contributed very little to the dataset.

Bealey (single mire system) data set

This comprised diatom relative abundances (%) from samples collected on the same day from 18 sites with pH in the range 5 to 6.5, in a mire pool system at Bealey Spur. For a description of the study area (including a map) and sample collection details see Kilroy et al. (2006) [II]. Briefly, we took composite substrate samples from approximately uniform water depths. Slides were prepared as above, then at least 600 valves were counted per sample, with identifications to species level where possible, using a range of texts (see Table II.1). Species were assigned endemic or non-endemic status, as above.

Temporal data set

Four pools (subsequently referred to as pools A, B, C and D) from the single mire system (above) were sampled at approximately fortnightly intervals from February 2002 to April 2004. A suite of environmental variables was measured on each sampling occasion. For site locations, refer to

Kilroy et al. (in revision [III]), and for details of sample collection (including environmental data variables, with collection and analysis methods) see Kilroy et al. (2006 [II]). Pool characteristics are summarized in Table V.1. For this temporal dataset, species counts were made on preserved subsamples rather than on prepared slides and we counted live cells (i.e. containing chloroplasts). Both quantitative data (counts or biovolume (1000 x μm^3) per mm^2 of substrate) and proportional data (%) were available. Species were assigned endemic or non-endemic status, as above.

Table V.1. Selected characteristics of the four sites with temporal datasets, showing means (with standard deviations) over the monitoring period. Different superscript letters indicate significant between-pool differences in that variable (ANOVA, P < 0.05, Bonferroni-corrected).

Pool:	A	B	C	D
Estimated area (m^2)	40	4400	700	1100
Water pH	5.3 (0.21)^a	6.5 (0.22)^b	6.3 (0.18)^c	6.7 (0.27)^d
Total dissolved phosphorus (μg/L)	1.6 (0.6)^a	1.3 (0.5)^{ab}	1.1 (0.4)^b	1.7 (0.4)^a
Water column chlorophyll *a* (μg/L)	2.05 (1.7)^a	2.63 (1.42)^{ab}	1.79 (1.2)^a	3.47 (2.35)^b
Benthic chlorophyll *a* (mg/m^2)	133 (55)^a	259 (68)^b	356 (132)^c	155 (53)^a
Number of diatom taxa	14.7 (1.9)^a	14.2 (1.3)^a	9.2 (1.4)^b	20.7 (2.1)^c
Simpson diversity index	5.43 (2.0)^a	3.33 (0.54)^b	1.83 (0.36)^c	5.74 (2.43)^d
% endemics	38.7 (15.3)^a	88.4 (5.6)^b	91.3 (3.9)^b	59.2 (13.5)^a

Data analysis

For all abundance–occupancy and abundance–persistence relationships, mean species abundances were calculated only from occupied sites or times (Gaston et al. 2000), using relative abundance data. Data for the single mire and temporal datasets were log-transformed. We used simple linear regression to test for significance of the relationships, and analysis of covariance (ANCOVA) to determine whether the endemic and non-endemic groups showed different relationships.

In the temporal dataset, core species were taken to be those that occurred on all 57 sampling occasions at a particular site. Intermediate species were those that occurred on at least 50 occasions (approximately 90%). We examined the frequency distributions of all species to distinguish true satellite species (having right-skewed distributions due to only occasional appearances) from intermediate species (approaching log-normal, which was seen in all core species). Temporal variability of each core and intermediate species was calculated as Population Variability (PV), which is the mean percentage difference between all combinations of observed abundances (Heath 2006). For a community-based measure of temporal variability, we also calculated diversity at each site, using a modified Simpson index,

$$\text{Simpson index} = 1 / \sum[(p_i)^2]$$

where p_i is the proportion of the community biovolume made up by species 1, 2, 3, …. *i*. This index was considered to provide a more appropriate measure of diversity than taxonomic richness as it takes into account the evenness of species distributions such that the index is equal to the number of species if all are present in the same proportion. Rare species are thus down-weighted. The index was also calculated separately for the non-endemic and endemic components of each community. Community variability was summarized as the coefficient of variation (CV) of each Simpson index time series. Because of the small size of diatoms (scale of μm) and rapid turnover of generations (Baars 1983), we considered that each sample was spatially independent.

For all three datasets, we assessed significance of the relationship between numbers of non-endemic and endemic taxa using simple linear regression. We used t-tests to look at differences in PV between endemic and non-endemic core taxa in the temporal datsets.

Responses to environmental variability

In an earlier analysis (Kilroy et al. in revision [III]) we showed that inter- (spatial) and intra-pool (temporal) differences were considerable with respect to a wide range of physico-chemical variables, but there was no clear difference in variability *per se* among the pools (unpublished data). We therefore looked for correlations between individual species and environmental gradients. Species–environment interactions were assessed by first generating Pearson correlation matrices between environmental variables (log-transformed as necessary) and logged abundances of core and intermediate species, the latter generally present in at least 90% of all samples and showing approximate log-normal distributions. Where relationships were significant, we examined the data further to determine the nature of the relationship (e.g., a seasonal pattern, or a sustained trend). Because species are unlikely to respond immediately to some environmental fluctuations, we repeated the procedure with a time lag, i.e., correlations were run on species abundances versus environmental values for the previous sampling occasion (mean 14.2 days apart).

Results

The regional dataset showed a positive interspecific abundance–occupancy relationship in that the species having high proportional occurrences invariably had high abundances, though species occurring in only a few sites could also have high abundances (Figure V.2). No widespread species had low mean abundance. Because of the triangular shape of the relationship, it was not possible to use regression to test for significance. However, endemic and non endemic taxa showed the same general pattern (Figure V.2). There was no relationship between numbers of endemic and non-endemic taxa across sites (Table V.2).

The single mire system dataset showed a clear positive abundance–occupancy relationship in which no species with low site occupancy had high mean abundance, and vice versa (Figure V.3). The relationship was stronger if maximum abundance was used rather than mean abundance, and

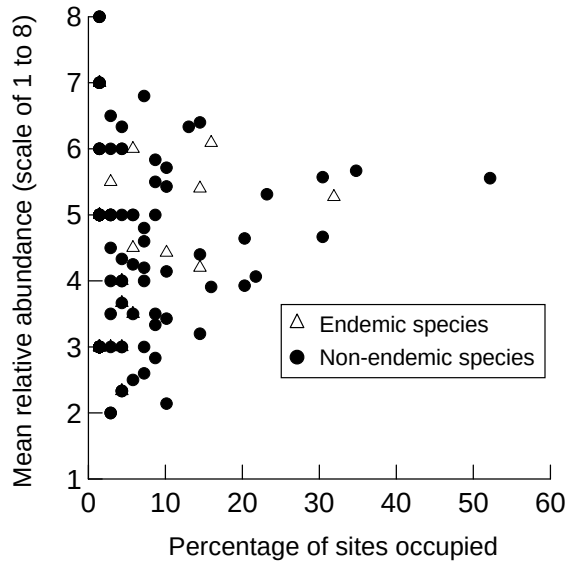


Figure V.2.
Abundance–occupancy relationship for benthic diatom species from subalpine mire pools in the South Island, New Zealand. Relative abundance was estimated using a visual scoring system (see text).

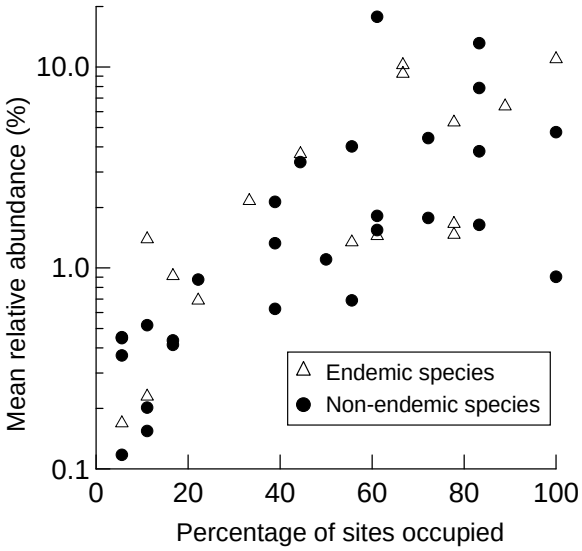


Figure V.3.
Abundance–occupancy relationship for benthic diatom species from 18 sites in a single subalpine mire-pool system. Refer to Table V.2 for details of regressions.

the regressions for endemic and non-endemic species were almost indistinguishable from that for the whole dataset and each other using both mean and maximum abundances (mean, no significant interaction P = 0.151, ANCOVA F = 0.233, P = 0.632; maximum, no significant interaction P = 0.927, ANCOVA F = 0.875, P = 0.355) (Table V.2). Again there was no relationship between endemic and non-endemic taxon richness across sites (Table V.2).

Species abundance–persistence plots on the temporal dataset suggested a visual gradient of partitioning of communities over the four sites into core, intermediate and satellite species. This was most pronounced in pool C, intermediate at B and A, and least pronounced at site D (Figure V.4). The differences were confirmed by examining inter-site differences in the distributions across species of proportion of sites occupied and mean relative abundances. Kolmogorov-Smirnov two-sample tests showed that both distributions in pool C significantly differed from those in pools A and D, and species abundance distributions in pools B and D significantly differed (Figure V.5).

Table V.2. Summary results of linear regressions used to test relationships listed in Figure V.1. Temporal abundance data were log (log)-transformed prior to analysis to conform to normality requirements. Significant relationships (P < 0.05) are highlighted in bold. A (=) in the "Distribution" column indicates non-significance in ANCOVA between endemics (E) and non-endemics (NE), i.e., the distributions are not different.

Dataset	Relationship	Distribution	R^2	P
Regional	Mean abundance vs. occupancy	all	No test possible	
	NE vs. E (sp. richness)	-	0.000	1.000
Local	Mean abundance vs. occupancy	all	**0.577**	**0.000**
	(log-transformed)	E (=)	**0.574**	**0.000**
		NE (=)	**0.563**	**0.000**
	Maximum abundance vs. occupancy	all	**0.688**	**0.000**
	(log-transformed)	E (=)	**0.633**	**0.000**
		NE (=)	**0.670**	**0.000**
	NE vs. E (sp. richness)	-	0.000	1.000
Temporal, A	Mean abundance vs. occupancy	all	**0.558**	**0.000**
	log-log-transformed	E (=)	**0.550**	**0.033**
		NE (=)	**0.545**	**0.004**
Temporal, B	Mean abundance vs. occupancy	all	**0.714**	**0.000**
	log-log-transformed	E	0.433	0.138
		NE	**0.831**	**0.000**
Temporal, C	Mean abundance vs. occupancy	all	**0.682**	**0.000**
	log-log-transformed	E	**0.592**	**0.045**
		NE	**0.812**	**0.000**
Temporal, D	Mean abundance vs. occupancy	all	**0.658**	**0.000**
	log-log-transformed	E (=)	**0.772**	**0.011**
		NE (=)	**0.771**	**0.000**
Temporal, A - D	NE vs. E (sp. richness)	-	**0.475**	**0.000**
	NE vs. E (mean sp. rich by pool)	-	0.656	0.122

Note that the species abundance distributions in pools A and B were close to being significantly different (P = 0.057).

Distribution plots for all species at each site showed the predicted log-normal patterns for all core species (present on all sampling occasions), and increasingly right-skewed for the intermediate and satellite species (data not shown). Linear regressions were all significant (Table V.2) on log-(log)-transformed data (this transformation necessary due to the extreme numerical dominance of the most abundant core species at all sites, *Kobayasiella* sp. A). Other core species were both endemic and non-endemic and also varied in size and habit (Table V.3). Linear regressions for

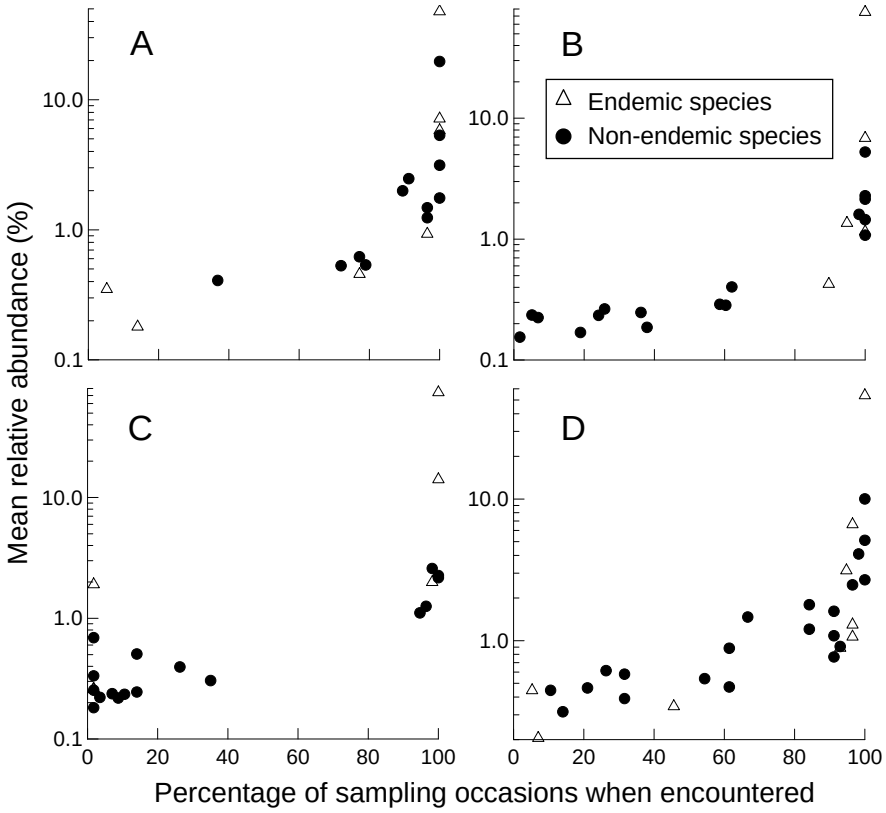


Figure V.4. Species abundance–persistence relationships for 83 benthic diatom species in 4 mire pools, over two years (57 sampling occasions). Relative abundance was estimated as counts of live diatoms. Endemic and non-endemic species are distinguished. Core species are taken to be those continuously present.

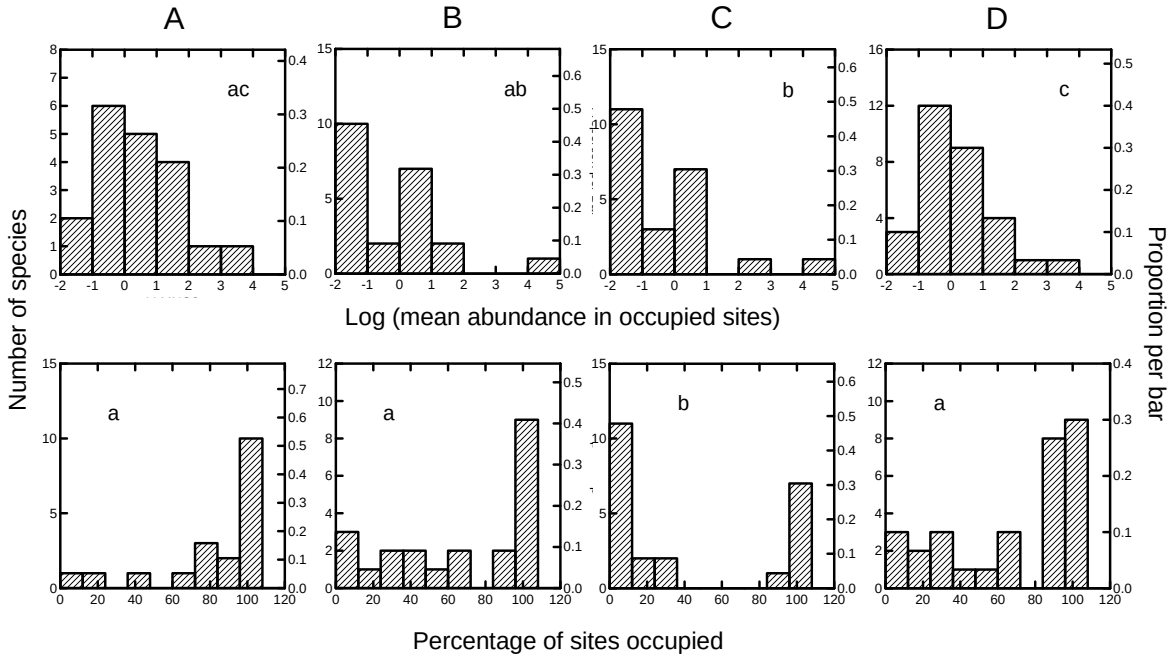


Figure V.5. Distributions of log (abundance) and percentage of sites occupied (i.e., species persistence) for species in pools A to D over 57 sampling occasions. Different lower-case letters indicate that the distributions are significantly different (Kolmogorov-Smirnoff two-sample tests, $P < 0.05$).

Table V.3. Temporal dataset: list of core benthic diatom species (occurring on 100% of sampling occasions) in each pool, in order of distribution, then total numerical abundance across all four sites. Rank abundances are shown for the community each pool. E = endemic taxon, NE = non-endemic. Size classes are according to biovolume (μm^3): vsmall, < 10; small 10 – <100; medium 100 – <1000; large >1000.

		Rank abundance				Species characteristics		
Species	Site:	A	B	C	D	distribution	size	habit
Kobayasiella sp. A		1	1	1	1	E	small	motile
Kobayasiella sp. B		3				E	small	motile
Eunophora cf. *oberonica*			2	2		E	large	non-motile
Encyonopsis sp. A		4				E	medium	motile
Amphora (*Eunophora*) *berggrenii*			7			E	large	motile
Eunotia bilunaris var. *mucophila*		2	5			NE	small	attached
Brachysira brebissonii		5	4			NE	small	motile
Chamaepinnularia spp.				3	2	NE	vsmall	motile
Eunotia spp.		6				NE	vsmall	attached
Kobayasiella parasubtilissima			3			NE	vsmall	motile
Encyonema neogracile			6	4	3	NE	small	motile
Frustulia cf. *magaliesmontana*		7				NE	medium	motile
Tabellaria flocculosa			8		4	NE	small	filaments

endemics and non-endemics differed most in pool B, where all the endemics present were core species. ANCOVA showed no significant difference between the regressions for endemics and non-endemics in pools A and D (pool A, no interaction, P = 0.585, ANCOVA F = 1.684, P = 0.213; pool D, no interaction, P = 0.525, ANCOVA F = 2.443, P = 0.130). For both pools B and C, the interaction terms were significant (P = 0.000, and P = 0.01, respectively. The endemic vs. non-endemic relationship was non-significant at individual sites over time, but data from all four sites combined showed a significant positive correlation (Table V.2). When the latter regression was repeated using mean abundances (i.e., n = 4) the relationship was non-significant (Table V.2).

Mean PV for endemic core species was significantly lower than that for non-endemics in pool C only (t = 4.448, P = 0.049, Figure V.6), though the difference at site B (t = 1.813, P = 0.174) was greater than that at sites A (t = 0.420, P = 0.692) and D (no test possible because n = 1 for endemics). The Simpson index calculated using numerical abundances was strongly influenced at all four sites by the overwhelming numerical dominance of the small species *Kobayasiella* sp. A. We therefore recalculated the index with species abundances weighted by their relative biovolumes. The overall patterns using the two calculations were similar, but the biovolume

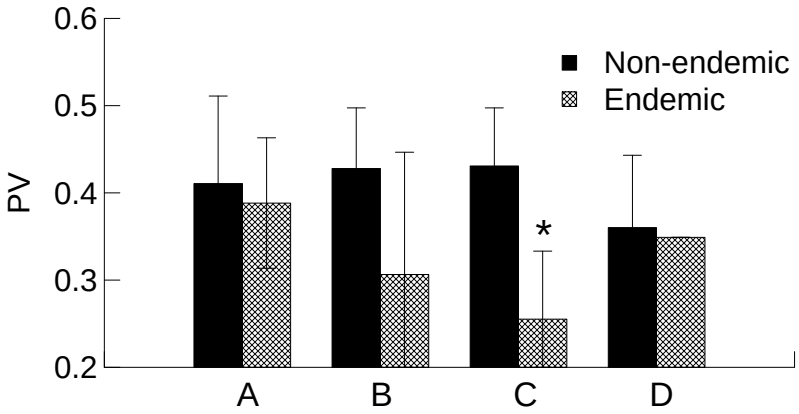


Figure V.6. Mean population variability (PV) (with standard deviations) for non-endemic and endemic core taxa at sites A to D. * significant difference between the two groups of taxa ($P < 0.05$).

method produced clearer relationships, which are presented here. The Simpson index differed significantly among sites (Table V.1), and the CV of the index for endemics was lower than that for non-endemics at all sites (Figure V.7). The nature of these differences in variability can be seen in time series plots of the Simpson index for endemic and non-endemic species groups at each site. At sites A and D there were clear seasonal fluctuations in the non-endemic group, which were absent from the non-endemic groups at sites B and C, and from the endemic groups at all four sites (Figure V.8).

Just one species showed a significant correlation between abundance and environmental variables at each of pools B and C, whereas pools A and D had four and five respectively including endemics and non-endemics (Table V.4). In all cases the species abundances fluctuated seasonally (data not shown).

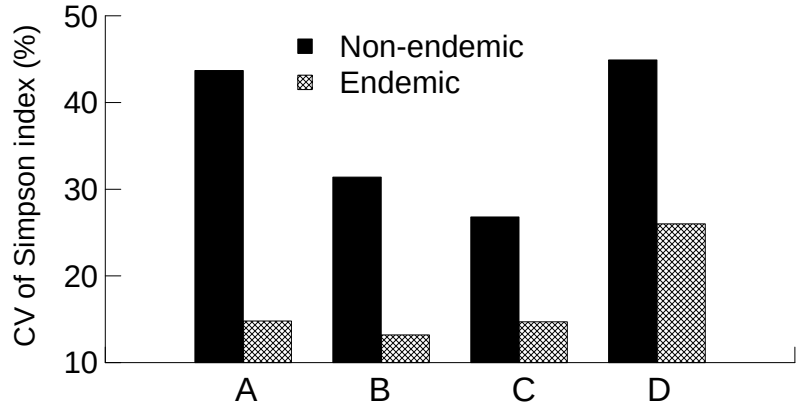


Figure V.7. Coefficients of variation of the Simpson index calculated for all species, endemic species and non-endemic species in four subalpine mire pools. The indices were calculated using species numbers weighted by biovolume, over 57 sampling occasions, approximately 14 days apart.

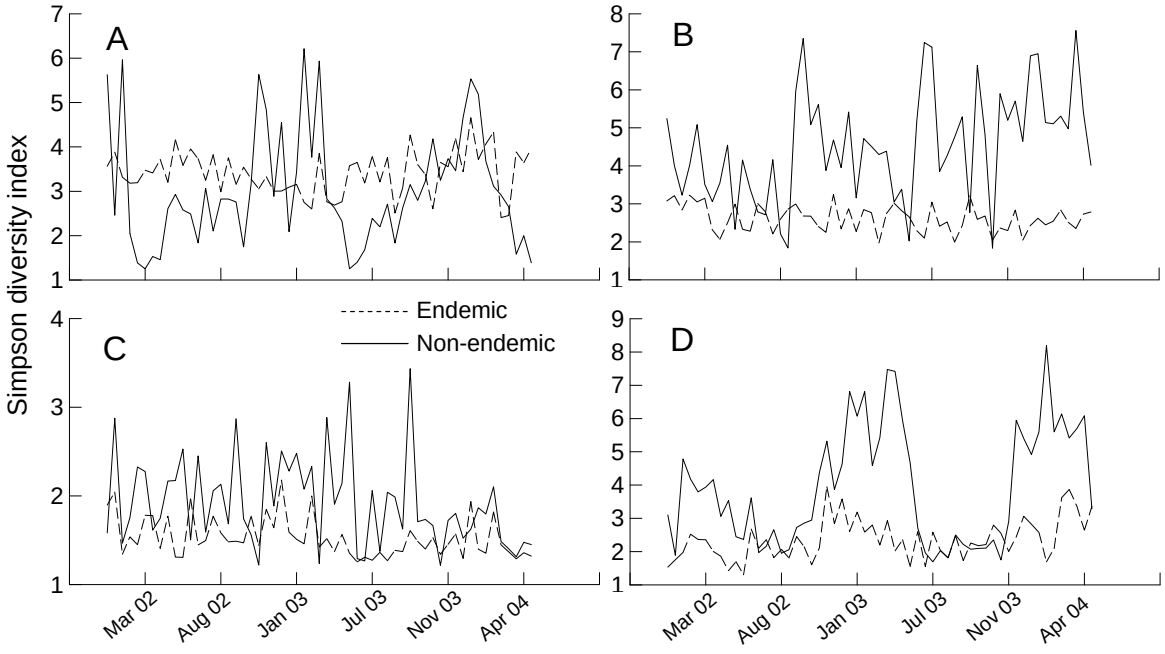


Figure V.8. Time series of the Simpson index calculated for endemic species and non-endemic species in four subalpine mire pools (A – D). The indices were calculated using species numbers weighted by biovolume, over 57 sampling occasions, approximately 14 days apart. Note the different scales on the y-axes of each plot.

Discussion

In this study we found that benthic diatoms in mire pools exhibited positive interspecific abundance–occupancy relationships, in common with many other organism groups (Gaston et al. 2000), including stream diatoms (Soininen and Heino 2005). Furthermore, the expected parallel relationship within individual communities over time (abundance–persistence) was also evident in four separate communities. Therefore the relationships found for stream diatoms elsewhere may indeed represent a general pattern in benthic freshwater diatoms (Soininen and Heino 2005).

The abundance–occupancy relationship is a component of the abundance–range size relationship, which is also pervasive, although less commonly documented (Gaston 2003). Thus, species with large geographic range sizes also tend to have high population densities. Applying this to diatoms we would expect that the most common non-endemic diatoms should be more abundant, on average, than any endemic taxa. However, we found that in both the South Island and Bealey datasets, endemic taxa were distributed throughout the entire range of abundances. Additionally, the endemic and non-endemic relationships at Bealey were identical. This suggests that the mechanisms driving the overall relationship are operating at a regional scale.

What causes positive abundance–occupancy relationships in general is still unclear, but they most likely can be attributed to a combination of processes (Gaston 2003). In diatoms,

Table V.4. Significant correlations between benthic diatom species abundances and environmental variables determined in four mire pools over 57 sampling occasions approximately 14 days apart. Probabilities are Bonferroni-corrected.

Pool	Species	Dist.	Environmental variable	*R*	*P*
A	*Pinnularia macilenta*	NE	Total dissolved N	-0.597	0.000
			Temperature (mean over prev. 10 d)	-0.506	0.009
			pH (lagged)	-0.466	0.043
	Neidium iridis	NE	Temperature (mean over prev. 10 d)	-0.554	0.001
	Kobayasiella sp. A.	E	log NO_3	-0.493	0.021
	Eunotia bilunaris v. *mucophila*	NE	log Total dissolved P (lagged)	0.477	0.027
			Total dissolved N	0.466	0.047
B	*Chamaepinnularia* spp.	NE	Conductivity	0.479	0.020
C	*Kobayasiella parasubtilissima*	NE	Dissolved organic carbon	-0.456	0.038
D	*Kobayasiella* sp. A.	E	log Dissolved reactive P	-0.599	0.000
			Conductivity (lagged)	-0.548	0.002
			log NH_4	-0.536	0.006
			Total dissolved N	-0.504	0.010
			Temperature (mean over prev. 10 d)	-0.466	0.041
	Encyonopsis sp. B	E	log NH_4	-0.596	0.000
			log Dissolved reactive P	-0.520	0.006
	Brachysira brebissonii	NE	Alkalinity	-0.531	0.003
	Navicula sp. A	E	log NH_4	-0.546	0.004
	Pinnularia sp. A	E	Alkalinity	-0.551	0.009
			Total dissolved N	-0.493	0.015

metapopulation dynamics (Leibold 2004) has been proposed as a likely mechanism driving patterns of local coexistence and high local diversity in diatoms (Soininen 2006). Assuming that all diatoms can disperse freely and randomly, those species with most propagules will remain common and widespread, and those with least will remain rare and sparse. Interspecific differences in dispersal ability are expected to accentuate this effect. Proponents of ubiquity in diatoms and other microbial groups (Finlay 2002) have assumed that all microorganisms disperse easily (that is why they are ubiquitous). At the same time, the mechanisms for dispersal are not at all clear. The most obvious long-distance dispersal medium is air, and undoubtedly this is important for dispersal in some algae (Sharma et al. 2007). However, few freshwater diatoms are known to possess desiccation-resistant stages that would permit long-distance dispersal by air (McQuoid and Hobson 1996). Therefore it seems unlikely that common non-endemic taxa are continuously arriving in great numbers in New

Zealand from a global metacommunity. Thus, the observed congruence of endemic and non-endemic abundance patterns in this study would be expected.

Positive abundance–persistence relationships at the community scale differed from those for stream diatoms (Soininen and Heino 2005) in that the core species tended to be very much more abundant than the intermediate and satellite species. The shapes of all four relationships may be partly a sampling artifact resulting from the long time series (e.g., see discussion in McGill 2003; and see Magurran 2007). Nevertheless, persistence differences would be expected between mire pools and streams because of the stable conditions and low species turnover in mire pools, compared to periodic disturbances and continuous upstream inputs of propagules in streams. In all four pools, the same endemic species (*Kobayasiella* sp. A) was numerically dominant, but complements of other core species were pool-specific, presumably due to inter-pool differences in environmental conditions (see below).

Endemic and non-endemic species showed similar abundance–persistence relationships in pools A and D only. These sites were also somewhat separated from sites B and C in their species distributions for abundance and persistence (Figure V.5), along a gradient of sites C, B, A, D (i.e., sites C and D were most different from each other). We noted other differences along the same gradient. For example, differences in population variability between endemic and non-endemic core taxa, as predicted by Glazier (1986), were greatest in pool C, with low PV in endemic species. Endemic species diversity (measured as the Simpson index for those species) was visually most variable in pool D. Variability of non-endemic species diversity followed the gradient C, B, A, D. Finally, species – environment relationships were evident for only a single species in pools C and B, but for multiple species in pools A and D. Fluctuations over time for these species indicated that all were responding to seasonal changes, which were clearly evident for the non-endemic species as a whole in pools A and D, but not in pools B and C. Lack of clear seasonal variability for the endemic community in any pool is consistent with observations by Glazier (1986). Some of these inter-pool differences are qualitative, but together they can be interpreted as a gradient of intra-community processes driving the species patterns, which were strongest in pool C and weakest in pool D.

Although diatoms are perceived to have high local diversity in general (Soininen 2006), our data show that this is not necessarily the case. At the community level in stable environments such as mire pools, we find that species with specialist environmental requirements can dominate. We suggest that they will coexist mainly with species with different requirements. For example, the same two endemic species were most abundant in pools B and C. *Kobayasiella* sp. A is a small, highly motile taxon, while *Eunophora* cf. *oberonica* is up to two orders of magnitude larger and, from observations of live material during the course of the study, appears to be non-motile and lives closely associated with other algae (cyanobacteria) in the pool substratum [IV]. Thus classical niche theory may explain their coexistence, as well as the more recent concept of the “spatial

storage effect". Spatial storage maintains that, in a permanently heterogeneous local environment, species with limited dispersal capabilities will concentrate in localities that are favourable (i.e., meet their specialist requirements) yet present fewer opportunities for colonization by other species (Snyder and Chesson 2003). Hence at a community level in these mire pools, these local processes dominate over the metacommunity patterns seen at larger scales. The four study pools appear to represent a gradient of predominance of the two coexistence processes. In this case diatom communities in pools that have a benthic system more open to the overlying water for nutrient exchange, as suggested by the stronger species–environment relationships in pools A and D, are also more open to random colonization by both endemic and non-endemic taxa. In contrast, pools B and C could be characterized by a more closed benthic system, with a high proportion of internal nutrient cycling leading to highly efficient usage by the resident endemic taxa [IV].

A positive relationship between numbers of endemic and non-endemic taxa within regions, for example, as reported for different types of beetle (Vilenkin and Chitakunov 2000, Fattorini 2007), is consistent with a common pattern of a strongly right-skewed unimodal distribution for interspecific range sizes (Gaston 2003). In other words, a few species have large range sizes and many have small range sizes (see Gaston 2003 for examples). If ubiquity is usual in micro-organisms, this could lead to a negative relationship between endemics (a few species occurring in exceptional environments) and non-endemics (most species). The fact that we found no endemic – non-endemic richness correlations at the regional and local metacommunity scales in mire pool diatoms indicates that even in environments most favourable for endemism in diatoms (Kilroy et al. 2007 [I]), numbers of endemic species are less than expected for macroscopic organisms. The lack of a positive relationship also indicates that the studied diatom communities made up of coexisting endemic and non-endemic species (i.e., "invaders") are not analogous to coexisting native and non-native species in larger organisms. In other words, we did not find that the most species rich communities also had highest numbers of endemic species, as noted in, for example, plants (Stohlgren 1999). At the local scale, we found that a few species with restricted range sizes can dominate, but non-endemic species were also present. This has been noted for other recently discovered likely endemic diatom species in New Zealand. For example, *Actinella aotearoia* dominated at least two communities in different locations (Sabbe et al. 2000; CK, unpublished observations), and an undescribed species of *Melosira* numerically dominated a rock seepage community (CK, unpublished observations). In both cases, recognised non-endemics were also present. A crucial difference between microbial organisms (such as diatoms) and larger organisms may be the time factor, as suggested by Foissner (2006). Although diatoms have to shown to be capable of rapid evolution (Theriot 1992), many modern species are recognizable in fossil material from, for example, the late Eocene (45 – 40 million years ago) (see review by Sims et al. 2006). Thus we can speculate that some non-endemic diatoms may be very old species, and may be present as a result of extremely rare dispersal events.

Returning to our initial analogy between non-endemic diatoms and NIS (including invasive species) this study suggests that at least in mire pools in the South Island of New Zealand, the presence of non-endemic diatoms in the same locality has no effect on the success of endemic species. Similar observations have been made on other species groups, e.g., mammals with different range sizes (Glazier and Eckert 2002), and native and exotic forest plants (Gilbert and Lechowicz 2005). A caveat to this is that the stability of the environment needs to be maintained since disturbances can dramatically change both habitat quality and invasibility (Huston 2004, IV). Thus, heterogeneity in this low-disturbance, low-productivity environment both allows endemic species to thrive in some localities, yet permits colonization and persistence of non-endemics in others (e.g., Davies et al, 2005; Melbourne et al. 2007). The community-scale mechanism that permits this is likely to be habitat specialization by the endemic species, allowing them to competitively dominate small parts of the environment.

2.VI Taxonomy of benthic diatoms from subalpine mire pools

Introduction

Although the algal floras of high-altitude bog and mire pool environments are well documented for some overseas locations (e.g., Scherer 1988, Mataloni 1999, Watanabe et al. 2000, Muñoz et al. 2003), they have received relatively little attention in New Zealand, with the exception of the desmids, for which there are comprehensive accounts (Croasdale and Flint, 1986, 1988; Croasdale et al. 1994). Apart from an early study by Skuja (1976), and one or two of the locations sampled by Foged (1979) descriptions of the diatom flora from these environments are lacking. This is also clear from reviews of diatom research in New Zealand (Cassie 1983, Cassie-Cooper 1994).

Bogs and mire pools are typically acidic, oligotrophic (usually dystrophic) environments and their algal species composition reflects this, being strongly related to pH and/or alkalinity (e.g., Negro et al. 2003, Kilroy et al. 2006 [II]). Algal communities may be dominated by cyanobacteria (Goldsborough and Brown 1991, Goldsborough and Robinson 1996), but diatoms and desmids are also important. At the genus level, diatom communities in bogs and mire pools tend to be similar worldwide (but see Kilroy et al. 2006 [II]). However, at the species level, these communities can be regionally distinctive (e.g., Flower 2005).

Here, I examine the taxonomy of common species found in a subalpine mire pool system in New Zealand. Species are grouped within genera in alphabetical order, with a brief introduction to each genus. An assessment is made of the geographical distribution of each species, with emphasis on the probability of restricted distributions (i.e., endemism).

Methods

Samples of benthic algae were collected from a range of pools within the Bealey Spur wetland area, near Arthur's Pass, South Island, New Zealand. Refer to Kilroy et al. (2006 [II]) for a detailed description of the site and collection methods. Subsamples for analysis of diatom communities were oxidised in concentrated sulphuric acid followed by hydrogen peroxide to remove all organic material, then repeatedly rinsed in distilled water. Drops of the resulting suspension of diatoms were dried onto coverslips and mounted onto glass slides using Naphrax (Northern Biological Supplies, UK). Slides were examined at x1000 on a Leica DMLB light microscope (LM) with differential interference contrast optics, and specimens photographed (usually >10 for each taxon) using a Zeiss Axiocam system. For each taxon, cell dimensions and stria density were determined from the photographs following recommendations in Anon. (1975). Further subsamples of diatom suspensions were mounted onto metal stubs, sputter-coated with platinum and examined under a Leica S440 scanning electron microscope (SEM). Where details could not be seen under LM,

measurements were made from SEM photographs (zero tilt)[1]. All species were identified, and/or compared with similar taxa using an extensive range of literature (see descriptions below). Terminology for diatom structure follows that in Ross et al. (1979).

Results

A summary of cell dimensions and general features for 28 common taxa from Bealey is presented in Table VI.1, along with cell dimensions of the same or similar taxa given in the literature, and an assessment of the likely cosmopolitan or endemic status of each taxon. Note that Table VI.1 shows a subset of the taxa listed in Table II.1 (pages 42-43) and that new information has resulted in a change to the species name assigned to some taxa. The changes are explained in the species descriptions.

Nine of the taxa were assessed as indistinguishable from cosmopolitan taxa. Five were so similar to one or more cosmopolitan taxa (or satisfactory species discrimination was lacking) that at this stage they must be considered as more likely to represent cosmopolitan taxa than taxa with restricted distributions. Two taxa, *Brachysira* sp. A and *Navicula* sp. A are assessed as undetermined as there is not enough information to be more decisive. These seven taxa all require further study.

Two taxa are in a distinctive genus, *Eunophora*, known only from Tasmania and New Zealand (Vyverman et al. 1998) and one of these appears to differ from other species currently known in that genus. A further species (*Frustulia cassieae*) has already been reported as probably endemic to the New Zealand / E. Australia region (Beier and Lange-Bertalot 2007). The remaining nine taxa appear to represent as-yet undescribed species. Because of the presence of known related taxa in Tasmania or other parts of the Southern Hemisphere, and/or distinctive morphological features, these are all assumed to be likely to be endemic to New Zealand, or to the New Zealand / Tasmania / Eastern Australia region. Detailed descriptions and justification for the geographical range assessment for each species follows.

[1] Note I have found that measurements made from SEM photographs are often questionable since the orientation of specimens can distort the images. Therefore inconsistencies with published counts based on SEM measurements are likely to be more significant than inconsistencies based on LM measurements.

Table VI.1 **Summary of dimensions and species characteristics of Bealey Spur wetland populations of 28 diatom taxa (in bold type, with genera arranged alphabetically, and species by abundance), along with data for populations of the same or comparable species from other locations. Under "Range", each taxon has been assessed as either cosmopolitan (C), probably cosmopolitan (C?), probably endemic (E?), endemic (E) or undetermined (U). Abundance groups (across 20 sites at Bealey) are: Abund. (in at least 12 sites, mean relative abundance in the top 12 sites > 10%); Common (at least 8 sites, density > 5%); Occas. (at least 4 sites, density > 1%); Rare (in < 4 sites OR mean relative abundance in the top 4 sites <1%).**

No	Genus	Species	Authority	Location	Length (μm)	Breadth (μm)	Stria density (/ 10 μm)	Special features / comments	Reference(s)	Range	Abund. at Bealey
1	**Brachysira**	**wygaschii**	**Lange-Bertalot**		**41 - 47.5**	**9.5 - 10**	**21 - 23**			**C**	**Abund.**
	Brachysira	wygaschii	Lange-Bertalot	Europe	30 - 65	7 - 12	20 - 24		Lange-Bertalot and Moser (1994)		
2	**Brachysira**	**brebissonii**	**Ross**		**14 - 32**	**5.3 - 6**	**26 - 27**			**C**	**Abund.**
	Brachysira	brebissonii	Ross	Cosmopol.	12 - 45	4.5 - 8	24 - 27		Lange-Bertalot and Moser (1994)		
3	**Brachysira**	**sp. A**			**14.5 - 21.5**	**7 - 8.5**	**24 - 27**			**U**	**Abund.**
	Brachysira	gravida	Shayler and Siver	USA	15 - 30	6 - 9	27 - 31		Shayler and Siver (2004)		
4	**Brachysira**	**microcephala**	**(Grunow) Compère**		**14 - 29**	**4.1 - 5.7**	**32 - 33**			**C**	**Common**
	Brachysira	microcephala	(Grunow) Compère	Cosmopol.	12 - 34	3 - 5 (7)	30 - 36		Wolfe and Kling 2001		
	Brachysira	neoexilis	Lange-Bertalot		12 - 34	3 - 5 (7)	30 - 36		Lange-Bertalot and Moser 1994		
5	**Brachysira**	**sp B**			**20 - 26**	**10.8 - 11.5**	**22 - 24**			**E?**	**Occas.**
	Brachysira	lehmanniae	Lange-Bertalot & Moser	South America	24 - 30	8 - 9.5	23 - 25	narrower cells	Lange-Bertalot and Moser 1994		
	Brachysira	hannae	(Reimer) Lange-Bertalot & Moser	USA	25 - 73	13 - 21	19 - 22	large	Patrick & Reimer 1966		
	Brachysira	arctoborealis	Wolfe & Kling	North America	17 - 31	7 - 10	19 - 25	narrower cells, central pore	Wolfe and Kling 2001		
6	**Brachysira**	**sp. C**			**19.5 - 31.5**	**5.7 - 6.3**	**30 - 32**			**E?**	**Occas.**
	Brachysira	procera	Lange-Bertalot & Moser	Cosmopol.	25 - 60	4.5 - 6	27 - 30	central raphe endings far apart in large specs	Lange-Bertalot and Moser 1994		
	Brachysira	styriaca	(Grunow) Ross	N. Hemis.?	14 - 50	5 - 8	27 - 28		Lange-Bertalot and Moser 1994		

No	Genus	Species	Authority	Location	Length (μm)	Breadth (μm)	Stria density (/ 10 μm)	Special features / comments	Reference(s)	Range	Abund. at Bealey
7	**Encyonema**	**neogracile**	**Krammer**		**34.6 - 42.9**	**5.8 - 7**	**12.5 - 15**			**C**	**Abund.**
	Encyonema	neogracile	Krammer	Cosmopol.	16 - 50	4.7 - 6.6	12 - 15		Krammer, etc		
8	**Encyonopsis**	**sp. A**			**44 - 54**	**7.4 - 8.7**	**10 - 13**	**undulating outline, wide axial area, slit-like areolae**		**E?**	**Abund.**
	Encyonopsis	blanchensis	Krammer	New Caledonia	77 - 87	10.5 - 12	11 - 13	similar outline and axial area	Krammer 1997		
	Encyonopsis	aequalis	(W. Smith) Krammer	Scotland, cos	30 - 55	7 - 9	11 - 13	Narrow axial area, round areolae	Krammer 1997		
9	**Encyonopsis**	**sp. B**			**13.2 - 24.5**	**3.1 - 3.8**	**28 - 30**			**E?**	**Rare**
	Encyonopsis	thienemannii	(Hustedt) Krammer	Java	10 - 25	3 - 4.2	28 - 30	similar, but striae not radiate throughout	Krammer 1997		
	Encyonopsis	krammeri	Reichardt	Europe	11.5 - 23.5	2.6 - 3.8	28 - 30	capitate, radiate striae	Krammer 1997		
	Encyonopsis	microcephala	(Grunow) Krammer	Europe	10 - 23	3.5 - 4.2	23 - 25	capitate	Krammer 1997		
	Encyonopsis	moseri	Krammer & Lange-Bertalot	Canary Is	11.5 - 21	2.9 - 3.5	24 - 25	too narrow	Krammer 1997		
	Encyonopsis	delicatissima	(Hustedt) Krammer	Sumatra	11 - 23	2.5 - 3	29 - 32	subcapitate, small	Krammer 1997		
	Encyonopsis	minuta	Krammer & Reichardt	Europe	8 - 17	2.8 - 3.5	24 - 25	too small, capitate	Krammer 1997		
	Encyonopsis	subminuta	Krammer & Reichardt	Europe	10 - 25	3.4 - 4.5	23 - 26	subcapitate, coarser striae	Krammer 1997		
10	**Eunophora**	**cf. oberonica / tasmanica**			**29 - 79**	**7.9 - 9.4 (valve)**	**To 36, 16 – 18 dorsally**	**Cells 20 – 24 μm wide**		**E**	**Common**
	Eunophora	oberonica	Vyverman & Hodgson	Tasmania	24 - 56	5.3 - 10	30 - 34, 13 - 21 dorsal.	Cells 12 – 18 μm wide	Vyverman et al. 1998		
	Eunophora	tasmanica	Vyverman & Sabbe	Tasmania	29 - 74	5 - 10	20 - 34	Cells 13 – 18 μm wide	Vyverman et al. 1998		
11	**Eunophora**	**berggrenii**			**41.6 - 67.3**	**9 – 10 (valve)**	**15 - 16**	**Cells 27 – 29.5 μm wide**		**E**	**Occas.**
	Amphora	berggrenii	Cleve	Arthurs Pass	65			Cell width 25 μm	Cleve 1880		
12	**Eunotia**	**bilunaris var mucophila**			**36 - 80**	**1.9 - 2.6**	**20 - 24**			**C**	**Common**
	Eunotia	bilunaris var mucophila	Lange-Bertalot, Norpel & Alles	Europe	10 - >70	1.9 - 3	20 - 28		Alles et al. 1991		
	Eunotia	bilunaris	(Ehrenberg) Mills	Europe	10 - 150	~3	20		Alles et al. 1991		

No	Genus	Species	Authority	Location	Length (μm)	Breadth (μm)	Stria density (/ 10 μm)	Special features / comments	Reference(s)	Range	Abund. at Bealey
13	**Frustulia**	**saxonica**			**58.2 - 96.2**	**14.8 - 20.6**				**C**	**Common**
	Frustulia	saxonica	Rabenhorst	Cosmopol.	28 - 105	18 - 20			Lange-Bertalot 2001, Beier and Lange-Bertalot 2005		
14	**Frustulia**	**sp. A**			**47.5 - 77**	**9.3 - 11.6**	**34**	**clear area at centre**		**E?**	**Common**
	Frustulia	pseudoundosa	Flower	Falkland Is	37 - 45	10 - 12	38		Flower 2005		
	Frustulia	crassinervia	(Brébisson) Lange-Bertalot & Krammer	?	30 - 50	10 - 15	36 - 40	similar fine structure	Lange-Bertalot and Metzeltin 1996		
15	**Frustulia**	**cf. magaliesmontana**			**51 - 62**	**7.9 - 8.7**	**39 - 40**	**areola density 37 - 38**		**C?**	**Common**
	Frustulia	cf. magaliesmontana	Cholnoky	West Coast, South Island	47 - 51	7 – 9	37 - 39	areola density 32 - 35	Beier 2005		
	Frustulia	pseudomagaliesmontana	Camburn & Charles	USA	27 - 44	5 – 6.5	40 - 48	areola density 36 - 56	Siver and Baskette 2005		
16	**Frustulia**	**cassieae**	**Lange-Bertalot & Beier**		**80 -113**	**10.7 - 14.4**	**29 - 31**	**Isolated dots in the centre**		**E**	**Occas.**
	Frustulia	cassieae	Lange-Bertalot & Beier	NZ, E. Aust	70 - 100	11 - 14	29 - 31	isolated dots in the centre	Beier 2005		
	Frustulia	elongatissima	Lange-Bertalot	?	110 - 127	13-15			Lange-Bertalot 2001		
	Frustulia	blancheana	Maillard in Moser et al.1995	New Caledonia	70 - 84	10 - 13.3	25 - 30		Moser et al. 1995		
17	**Kobayasiella**	**sp. A**			**22 - 41**	**5.5 - 6.3**	**38 - 39**	**lanceolate, not parallel outline**		**E?**	**Abund.**
	Kobayasiella	acidophila	Vanhoutte	Tasmania	24.7 - 31.2	4.6 - 5.5	34 - 42		Vanhoutte et al. 2004		
	Kobayasiella	subtilissima	(Cleve) Lange-Bertalot		18 - 38	3.5 - 6	40 - 42	Often parallel	Kobayasi and Nagumo 1988		
18	**Kobayasiella**	**sp. B**			**44 - 47.5**	**7.7 - 8.4**	**39**			**E?**	**Occas.**
	Kobayasiella	madumensis	(Jorgensen) Lange-Bertalot	Europe	33	6.0 - 7.0			Lange-Bertalot 1996		
	Kobayasiella	krasskei	(Metzeltin & Lange-Bertalot) Lange-Bertalot	South America	44 - 50	8.4 - 8.7	27 - 28		Metzeltin and Lange-Bertalot 1998. Lange-Bertalot 1999		
19	**Kobayasiella**	**parasubtilissima**	(Kobayasi & Nagamo) Lange-Bertalot		**22 - 24**	**3.8**	**??**			**C?**	**Occas.**
	Kobayasiella	parasubtilissima	(Kobayasi & Nagamo) Lange-Bertalot	Europe	22 - 34	3.5 – 4.5	40 - 44		Kobayasi and Nagumo (1988)		

No	Genus	Species	Authority	Location	Length (μm)	Breadth (μm)	Stria density (/ 10 μm)	Special features / comments	Reference(s)	Range	Abund. at Bealey
20	**Navicula**	**sp. A**			**42 - 52**	**9 - 10**	**10 - 13**		**???**	**U**	**Rare**
21	**Neidium**	**iridis**	**(Ehrenberg) Cleve**		**89 - 100**	**21 - 22**	**18**			**C**	**Common**
	Neidium	iridis	(Ehrenberg) Cleve	USA	50 - 190	16 - 40	14 - 18		Patrick & Reimer 1979		
	Neidium	iridis	(Ehrenberg) Cleve	Europe					Krammer & Lange-Bertalot 1997		
22	**Pinnularia**	**macilenta**	**Ehrenberg**		**67 - 98**	**12 - 13.2**	**8.5 - 10**			**C?**	**Occas.**
	Pinnularia	macilenta	Ehrenberg	Guyana, Europe, NZ	60 - 134	12 - 15.5	8 - 10		Krammer (2000)		
	Pinnularia	subgibba	Krammer		60 - 100	10 - 12	8 - 9		Krammer (2000)		
23	**Pinnularia**	**sp. A**			**63 - 94**	**13.1 - 15.5**	**7 - 9.5**		**???**	**E?**	**Occas.**
24	**Pinnularia**	**biceps**	**Gregory**		**60.5 - 77**	**12.3 - 13**	**9.5 - 11**			**C**	**Occas.**
	Pinnularia	biceps	Gregory	Scotland	48 - 85	11 - 13	9 - 13		Krammer (2000)		
25	**Stenopterobia**	**delicatissima**			**67 - 77**	**4.2 - 4.6**	**25 - 27**	**65 - 73 fibulae**		**C**	**Occas.**
	Stenopterobia	delicatissima	(Lewis) Brebisson ex Van Heurck	Cosmopol.	30 - 100	3.5 - 9	18 - 27	40 - 75 fibulae	Krammer & Lange-Bertalot 1997		
26	**Stenopterobia**	**curvula**			**145 - 180**	**6.1 - 7.1**	**21 - 22**	**35 - 40 fibulae, capitate, rhombic apices**		**C?**	**Occas.**
	Stenopterobia	curvula	(W. Smith) Krammer	Cosmopol.	70 - 280	6 - 9	18 - 24	30 - 60 fibulae	Krammer & Lange-Bertalot 1997		
27	**Stenopterobia**	**sp. A**			**86 - 140**	**4.4 - 5.5**	**25 - 27**	**50 – 55 fibulae, finely tapered ends**		**E?**	**Occas.**
	Stenopterobia	densistriata	(Hustedt) Krammer	Cosmopol.?	63 - 110	4.5 - 7	26 - 30	40 - 60 fibulae, bluntly tapered ends	Krammer & Lange-Bertalot 1997		
28	**Tabellaria**	**flocculosa**						**Very variable shape and size**	Krammer & Lange-Bertalot 1997	**C?**	**Common**
	Tabellaria	flocculosa	Roth (Kützing)	Cosmopol.				Very variable			

Genus *Brachysira*

The genus *Brachysira* was first named in 1833 with the type species *B. aponina* Kützing (see Van Landingham 1968, p. 568). This species was subsequently transferred to *Navicula*, and *Brachysira* was not re-established until 1981 by which time related species had been assigned to both *Navicula* and *Anomoeoneis* (Round and Mann 1981). *Brachysira* species are especially common in oligotrophic lakes and bogs (Round et al. 1991). Lange-Bertalot and Moser (1994) discussed 69 *Brachysira* taxa (67 species), many of which were new species separated from about 15 taxa known up until that time. About 25 of the 69 taxa appear to be endemic to New Caledonia. Several new species of *Brachysira* have been described since the 1994 study (e.g., Souza and Compère 1999, Wolf and Kling 2001, Shayler and Siver 2004). *Brachysira* was numerically the most common genus in the material from Bealey (Kilroy et al. 2006 [II]). At least eight species were distinguished. The six most common are dealt with below in order of abundance.

Brachysira wygaschii Lange-Bertalot (Figure VI.1)

Description of Bealey material: Valves lanceolate to rhombic-lanceolate tapering to narrowly rounded tips. Length: 41 – 47.5 μm, breadth 9.5 – 10 μm, striae 21 - 23 per 10 μm at the centre of the valve. Raphe slightly curved at the centre and strongly curved at the distal ends, to the same side externally, but to opposite sides internally (Figure VI.1b, c). Narrow axial area expanded to a rhombic central area. Striae strongly radial to the raphe ends. Areolae typical for the genus. Very clear Voigt fault (unilateral discontinuity in the striae) at about two-thirds distance from the centre to the ends.

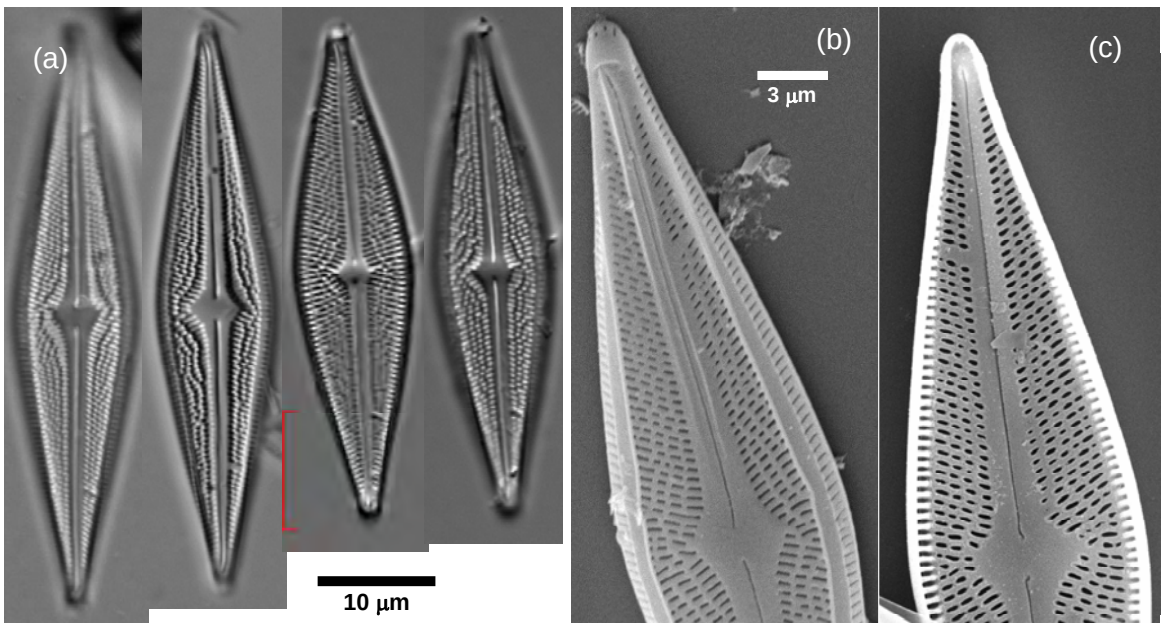


Figure VI.1 *Brachysira wygaschii*. (a) LM, Size declination; (b) SEM, external view; (c) SEM, internal view.

Comments: In SEM the Bealey specimens show features consistent with those illustrated in Lange-Bertalot and Moser (1994, p. 106), though longitudinal ridges either side of the raphe do not always continue to the centre (e.g., Fig. VI.1b) as shown in the single SEM illustration in Lange-Bertalot and Moser (1994). Wolfe and Kling (2001) illustrated a similar difference between populations of *B. brebissonii* from different locations but evidently did not consider it taxonomically significant. *B. wygaschii* has been reported from Scandinavia, Southeast Asia, Australia and South America (Lange-Bertalot and Moser 1994), thus appears to be truly cosmopolitan. The Bealey specimens are identical to a species identified as *Anomoeoneis serians* var. *acuta* Hustedt in the North Island (Foged 1979), which is synonymous with *B. wygaschii*.

***Brachysira brebissonii* Ross ssp. *brebissonii* (Figure VI.2)**

Description of Bealey material: Valves rhombic-lanceolate to elliptical-lanceolate with bluntly rounded ends. Length: 14 – 32 μm, breadth 5,3 -6 μm, striae 26 - 27 per 10 μm at the centre of the valve. Straight raphe in very narrow axial area, expanded rhombic-shaped central area. Striae moderately radial throughout, sometimes straight or weakly convergent at the poles. Usually only 2-3 areolae per stria towards the apices. Clear Voigt fault at about two-thirds distance from the centre to the ends.

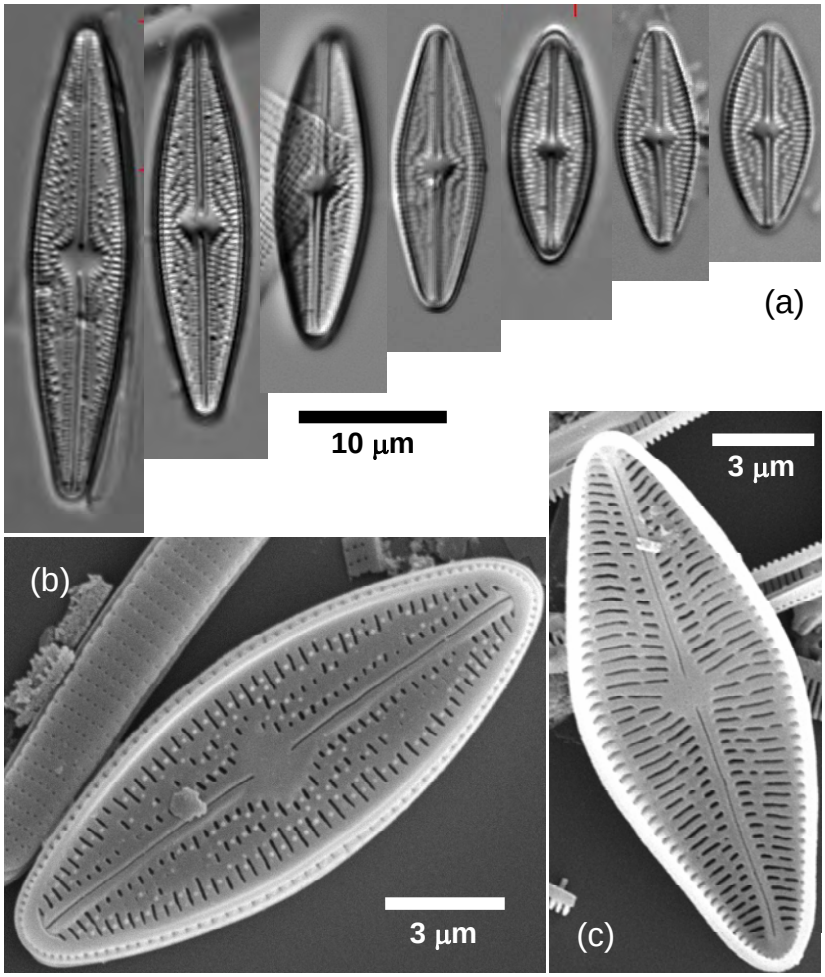


Figure VI.2
Brachysira brebissonii ssp. *brebissonii*.
(a)LM, size declination;
(b) SEM, external view;
(c) SEM, internal view.

Comments: The species *B. brebissonii* Ross has been applied to a variety of forms, which Lange-Bertalot and Moser (1994) considered to be "morphotypes or ecotypes [of] geographic or local variants of established taxa." According to Lange-Bertalot and Moser (1994), this species is unmistakeable in Europe. Populations in other continents have equivalent structure and dimensions, though tropical representatives may have striae divided into more areolae (lineolae). The taxon at Bealey conforms to the description of *B. brebissonii* ssp. *brebissonii* in Europe and North America (e.g. Wolfe and Kling 2001).

***Brachysira* sp. A (Figure VI.3)**

Description of Bealey material: valves elliptical to rhombic with wide, swollen mid-regions, and concave margins narrowing to protracted, rounded apices. Length: 14.5 – 21.5 μm, breadth 7 – 8.5 μm, striae 24 – 27 per 10 μm at the centre of the valve, lineate, comprising 1 – 3 (4) elongated areolae. Striae radiate throughout most of the valve, tending to parallel at the apices. Straight raphe (may be very slightly curved at the centre) in very narrow axial area with a clear round to rhombic central area 1 – 2 μm across.

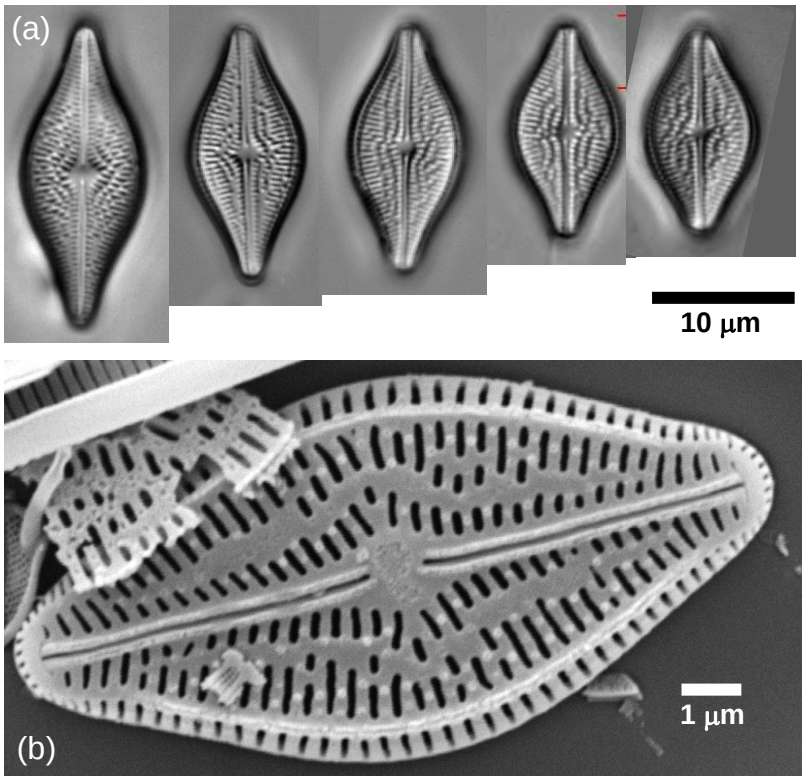


Figure VI.3
Brachysira sp. A
(a) LM, size declination
(b) SEM, external valve view

Comments: This species was very common (20 – 30% by cell numbers) in some pools at Bealey, but relatively rare in all four pools included in the detailed studies (< 2.5% of cells) (i.e. in pools A-D in Papers III to V). The species was tentatively identified as a form of *Brachysira brebissonii* Ross in Kilroy et al. (2006 [II]) on the basis of a provisional identification of a similar species

illustrated in Lange-Bertalot and Moser (1994; see page 192). The latter specimens have since been assigned to a new taxon, *Brachysira gravida* (Shayler and Siver 2004). Valve shape and dimensions of the Bealey population fall within the range of *B. gravida* (Table VI.1), but stria density was lower in the Bealey specimens (range barely overlapping). Therefore this taxon cannot be unequivocally assigned to *B. gravida* and further study is needed to establish whether it represents a different (and therefore potentially endemic) taxon.

***Brachysira microcephala* (Grunow) Compère (Figure VI.4)**

Description of Bealey material: Valves lanceolate, elliptical to rhombic-lanceolate usually with abruptly reduced ends, rostrate to weakly capitate. Length: 14 – 29 µm, breadth 4.1 – 5.7 µm, striae approx. 32 – 33 per 10 µm at the centre of the valve. Straight raphe in very narrow axial area, small, round or rhombic-shaped central area. Striae radial throughout. Voigt fault evident in SEM only.

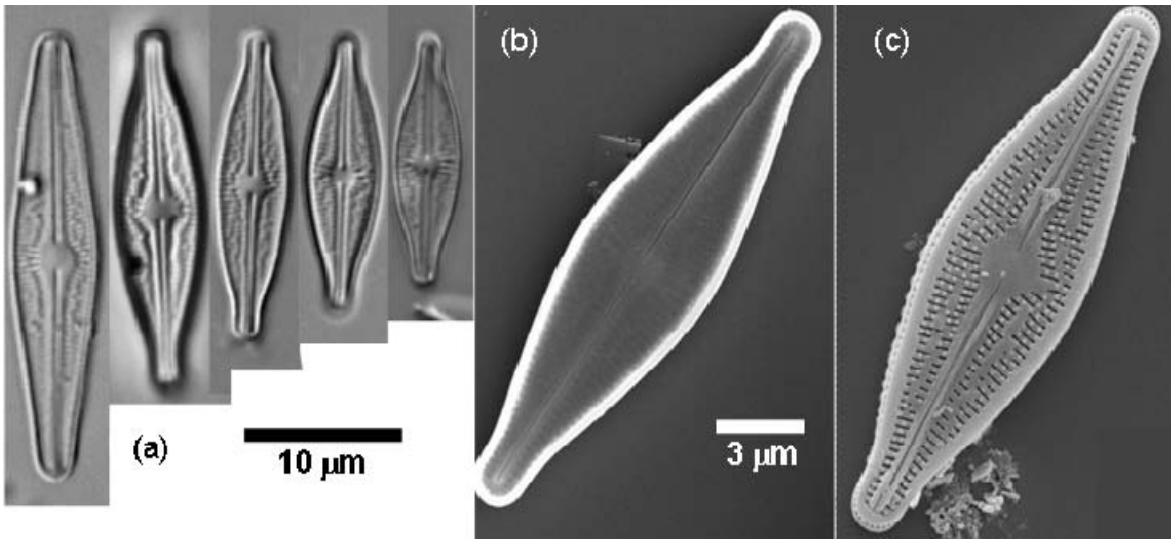


Figure VI.4 *Brachysira microcephala*. (a) LM, size declination; (b) SEM,internal view; (c) SEM, external view.

Comments: In Kilroy et al. (2006 [II]), this species was identified as *Brachysira neoexilis* Lange-Bertalot on the basis of correspondence in dimensions, outline and stria density. The original description of *B. neoexilis* was accompanied by illustrations of populations from Europe, Australia, Sumatra, Namibia, etc. (Lange-Bertalot and Moser 1994). A subsequent study of the same species from the USA pointed out the synonomy of this taxon with an existing species, *B. microcephala* (Wolfe and Kling 2001). These authors also stressed "considerable morphological variability in *B. microcephala*" with a continuum of forms ranging from capitate to lanceolate, which is also seen in the Bealey populations (Figure VI.4).

***Brachysira* sp. B (Figure VI.5)**

Description of Bealey material: valves broadly rhombic, occasionally with slightly protracted apices. Length: 20 – 26 μm, breadth 10.8 – 11.5 μm, striae 22 – 24 per 10 μm at the centre of the valve, lineate, comprising up to 6 irregularly elongated areolae. Striae radiate throughout the entire valve, except the last one or two at the apices, which are straight. Straight raphe in very narrow axial area with a more or less round central area 1.5 – 2.5 μm across.

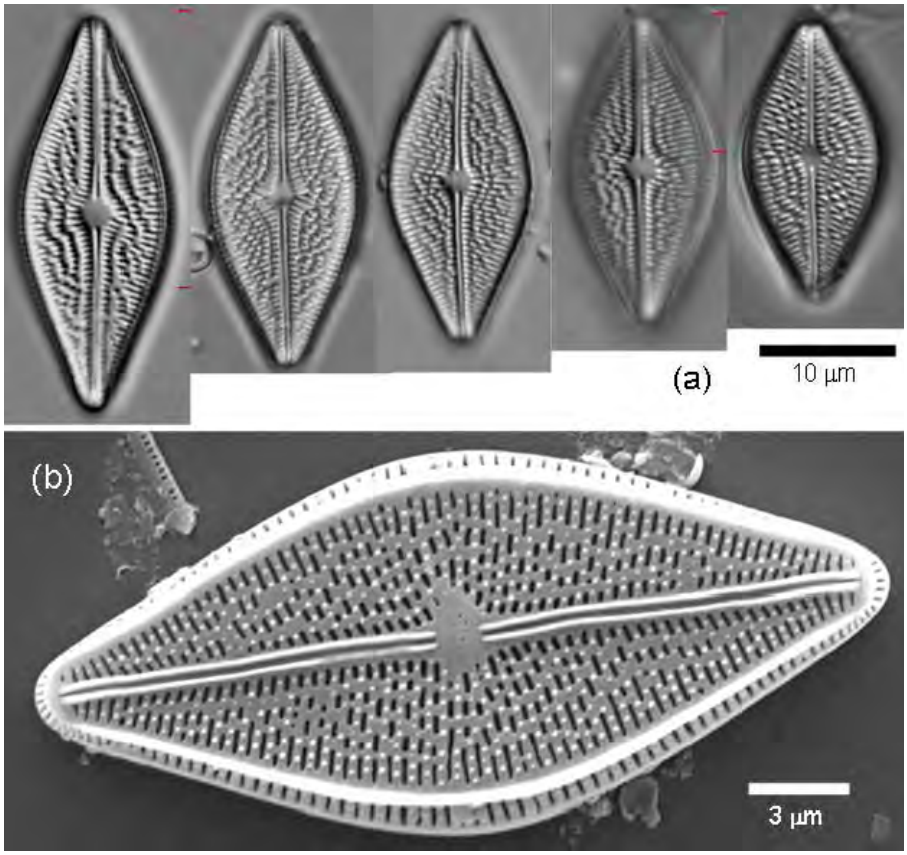


Figure VI.5
Brachysira sp. B.
(a) LM, size declination;
(b) SEM, external valve view.

Comments: In Kilroy et al. (2006 [II]), this *Brachysira* species was compared with *B. lehmanniae* Lange-Bertalot and Moser, which was described from high-altitude acidic waters in Columbia, South America (Lange-Bertalot and Moser 1994). The Bealey species resembles *B. lehmanniae* in length and stria density, but is broader and has a consistently larger central area. It is therefore unlikely to represent the same taxon. *Brachysira* sp. A also resembles *B. hannae* (Reimer) Lange-Bertalot and Moser in both outline and stria density, but the latter species is much larger (see *Anomoeoneis follis* var. *hannae* Reimer, in Patrick and Reimer 1966) (non-overlapping size ranges). A similar rhombic species, *B. arctoborealis*, has been described from acid lakes in North America. This species is always narrower than the Bealey species (Table VI.1) and usually has a distinctive enlarged areola at the centre (Wolfe and Kling 2001).

This species occurred in >50% of the pools sampled at Bealey with no clear pH preference. Densities were low (<1% of valves) in most cases, but exceeded 4% in two pools. This taxon has

also been observed in other similar habitats in the Bealey – Arthur's Pass area. It is assumed to represent an undescribed and possibly endemic taxon.

***Brachysira* sp. C (Figure VI.6)**

Description of Bealey material: Valves lanceolate, with swollen central region tapering to narrow apices. Length: 19.5 – 31.5 μm, breadth 5.7 – 6.3 μm, striae 29 – 31 per 10 μm, radial throughout. Straight raphe in very narrow axial area, opening to an elongated to oval central area, with the raphe endings set relatively far apart in larger specimens. Voigt fault not evident, even in SEM.

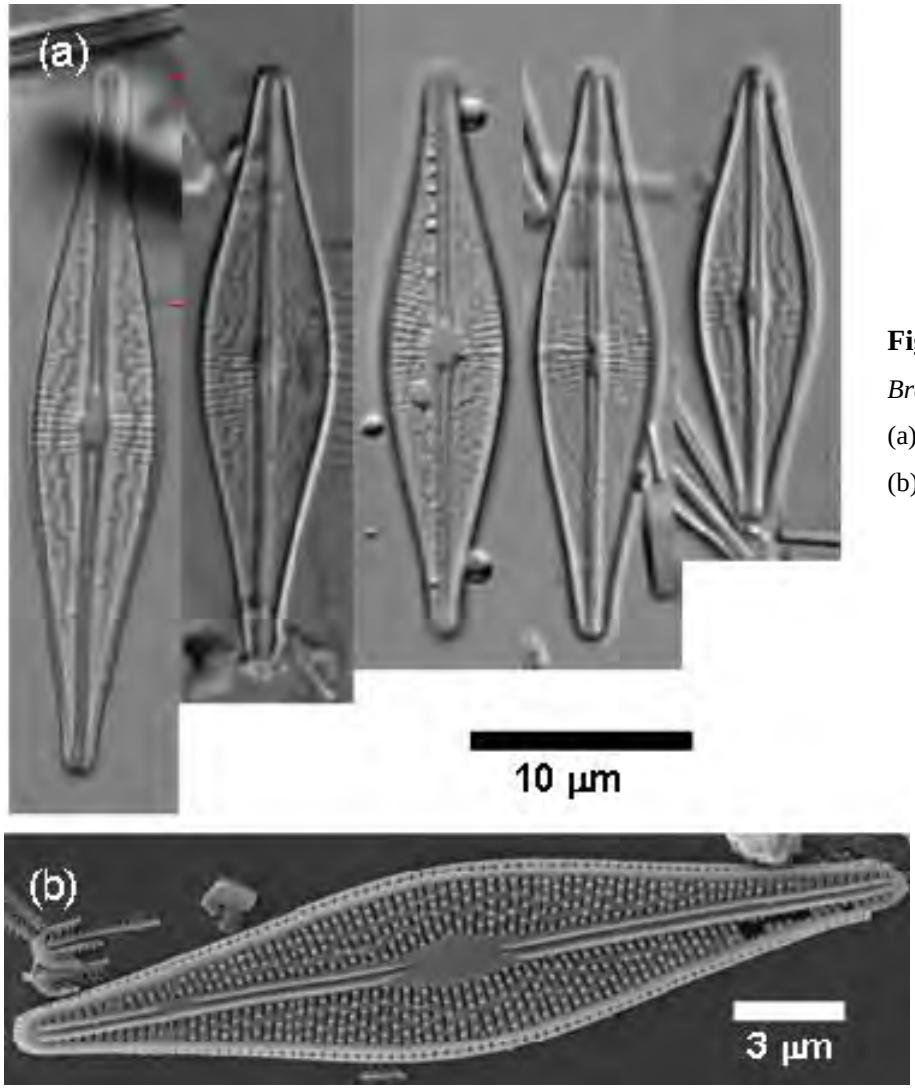


Figure VI.6
Brachysira sp. C.
(a) LM, size declination;
(b) SEM, external valve view.

Comments: This species was one of the less common of the *Brachysira* species identified from the Bealey material and occurred at only 6 sites (Kilroy et al. (2006) [II]). It was initially assigned to *B. styriaca* (Grunow) Ross on the basis of correspondence of the specimens located at that time with illustrations in Lange-Bertalot and Moser (1994). Examination of further specimens has shown that the Bealey species has clearer affinities with *B. procera* Lange-Bertalot & Moser and *B. neoexilis*

Lange-Bertalot in its fine striation, elongated central area. *B. procera* also has widely separated central raphe endings in larger specimens. The fine structure is also similar (compare Figure VI.6b with Plates 6 and 9 in Lange-Bertalot and Moser 1994). However, the swollen outline of the Bealey species is very different from either *B. procera* or *B. neoexilis*. No specimens approached the maximum size of 60 μm quoted for *B. procera* (Lange-Bertalot and Moser 1994), yet all were near to or exceeded the maximum width for that taxon (see Table VI.1). No other more similar species has been located to date, therefore it is concluded that this may represent an undescribed and possibly endemic taxon.

Genus *Encyonema* Kützing

Encyonema was first erected in 1833 but almost immediately became obsolete as taxa were transferred to the similar genus *Cymbella* Agardh, which was established in 1830. The fundamental differences between species related to the type specimens of *Encyonema* and *Cymbella* (i.e., the original concepts of these genera) were not acknowledged again until the 1980s (Krammer 1982). Since then many taxa have been reinstated in or transferred to *Encyonema*. The most abundant species in the Bealey samples was indistinguishable from a very common cosmopolitan species of *Encyonema*.

Encyonema neogracile Krammer (Figure VI.7)

Description of Bealey material: Valve dorsiventrally asymmetrical, smoothly rounded dorsally, straight or slightly convex at the centre ventrally, with the ends slightly deflected downwards. Length: 34.6 – 42.9 μm, breadth 5.8 – 7 μm, 12.5 – 15 per 10 μm at the centre of the valve, increasing in density towards the ends, and also becoming slightly divergent, especially ventrally. Typical *Encyonema* raphe curved upwards centrally and deflected downwards at the apices. Apical area is narrow and more or less parallel; there is always a wider central area. Many specimens have a single dorsal stigma, which varies from being barely distinguishable, except as an extension of the central stria, to fairly clear, the former being more common.

Comments: In all respects, this taxon is consistent with the initial description of *Encyonema neogracile* (Krammer 1997a). The fine structure is also consistent with that described for *Cymbella gracilis* (Ehrenberg) Kützing (= *Encyonema gracile*). In particular, the structure of the intermissio (internal dorsal notch at the central raphe endings), helictoglossae (internal thickened silica at the distal raphe endings) and internal striae /alveolae structure match those illustrated in Krammer (1982). Note that *Encyonema gracile* has been split into several different species, of which *E. neogracile* is one (Krammer 1997a). The type location of this taxon is Inarisee, Finnish Lapland,

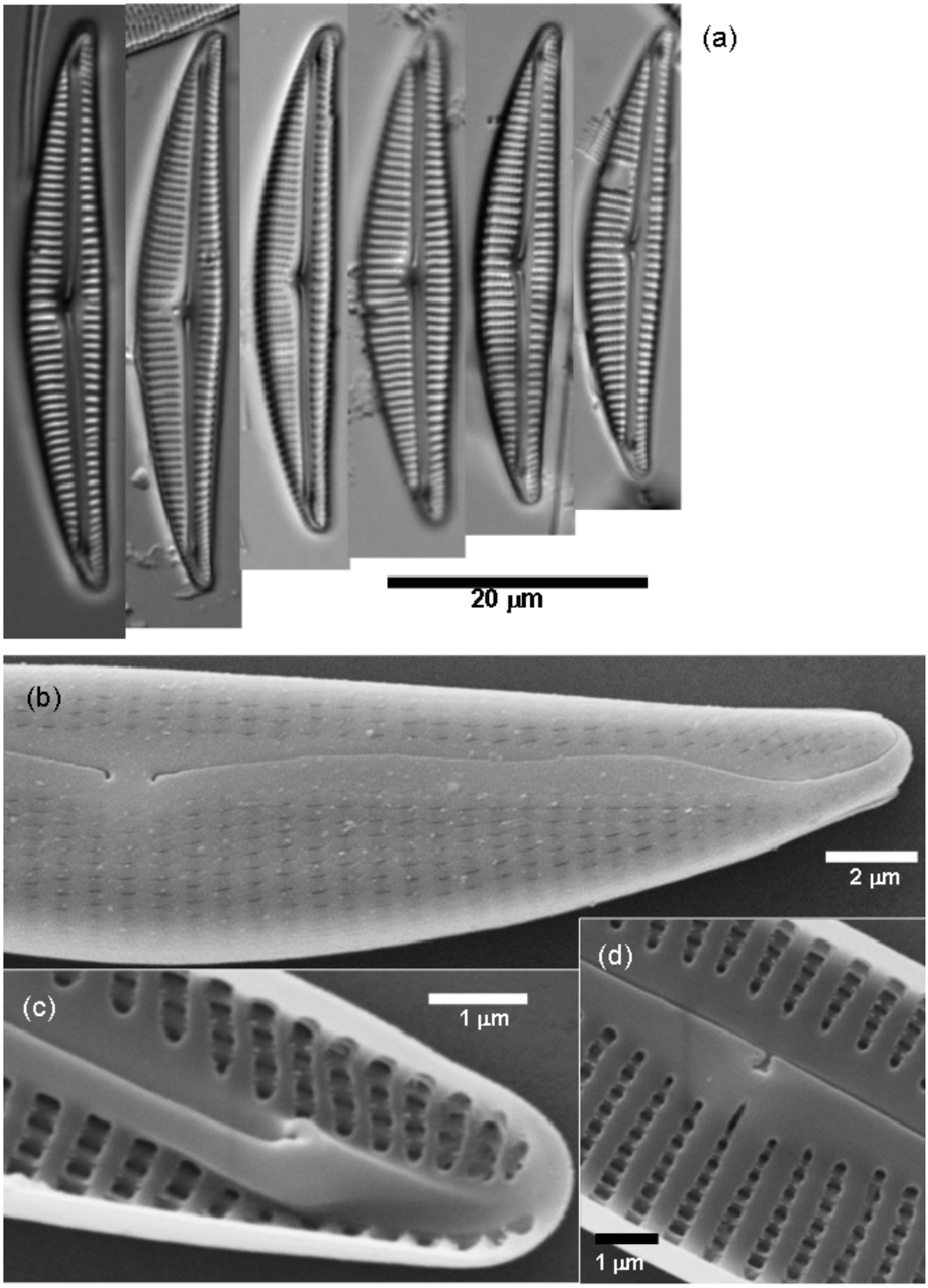


Figure VI.7 *Encyonema neogracile*. (a) LM, size declination; (b) SEM, external valve view; (c) SEM, internal view, detail of helictoglossa; (d) SEM, internal view, detail of intermission and internal stigma.

and its distribution is stated to be “Broad: Cosmopolitan…”. This species was very common throughout the Bealey wetland area, and was mainly confined to the less acidic sites (pH > 5.6).

Genus *Encyonopsis* Krammer

Encyonopsis was erected recently to encompass a group of taxa previously assigned mainly to *Cymbella*, which shared the following major characteristics (Krammer 1997b):

- in most cases an outline that is only slightly or not asymmetrical dorsi-ventrally (unlike most other *Cymbella* taxa), in other words, almost naviculoid;
- a centrally placed raphe, with internal and external fissures parallel;
- raphe similar to *Encyonema*: the central raphe endings or at least the central pores lie dorsally, and the terminal fissures are bent towards the ventral side. Terminal fissures generally question-mark, sickle- or bayonet-like, not comma-like as in *Encyonema*.

At least three taxa from Bealey were identified as belonging to *Encyonopsis*, though only one was common. The second most common was present in two pools and made up <2% of the communities there.

Encyonopsis sp. A (Figure VI.8)

Description of Bealey material: Valve more or less symmetrical dorsiventrally, lanceolate with slightly undulating outline, convex at the centre. Narrow apices, subcapitate, rounded to subrostrate, sometimes slightly curved to the ventral side. Length: 49 – 54 μm; breadth: 7.4 – 8 μm; striae: 11 – 12.5 per 10 μm at the centre of the valve, radiate at the centre to parallel and sometimes slightly convergent at the apices; spacing and orientation at the centre of the valve may differ on the two sides and is quite variable among specimens. In SEM, the individual areolae making up the striae are longitudinally oriented slits, about 50 per 10 μm. Raphe undulating, deflected towards the dorsal side at the centre, and curving dorsally to the apices, then downwards. Apical area is narrow at the apices, widening to a roundish central area; no stigmata (isolated puncta).

Comments: In II, this species was compared with *E. blanchensis* from New Caledonia, which is similar in shape and central area, but is larger and has coarser striae (Krammer 1997b, Moser et al. 1998). The overall shape, dimensions and stria density in this taxon also correspond with those described for *E. aequalis* (W. Smith) Krammer (Krammer 1997b). Differences are: (1) the Bealey taxon has a more marked undulating margin, rather than the rounded margin seen in *E. aequalis*; (2) the axial area tends to be wider in the Bealey taxon (although some published illustrations of *E. aequalis* also show a wider area, e.g., Krammer (1997b), Pl. 167/8); (3) in SEM, *E. aequalis* is described as having “very small, round stomata” (Krammer 1997b), in contrast to the slits seen in the Bealey taxon (Figure VI.8e), which are also much denser (50 per 10 μm, as opposed to 36-40 in *E. aequalis*.

No similar *Encyonopsis* species has been located in the available literature. While *E. aequalis* and the Bealey taxon superficially resemble each other, differences in outline and central area seen

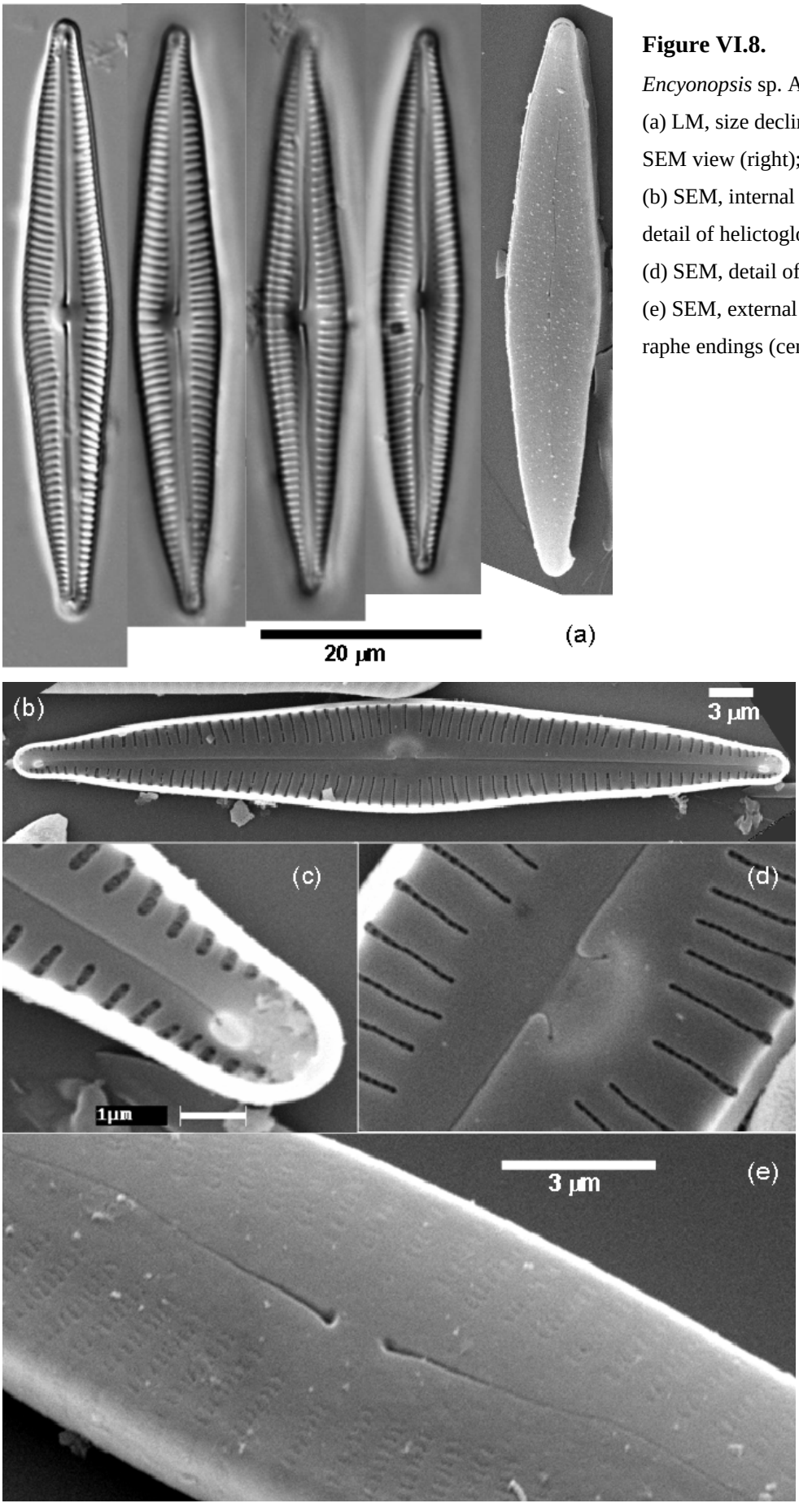


Figure VI.8.

Encyonopsis sp. A

(a) LM, size declination, with an exterior SEM view (right);

(b) SEM, internal valve view; (c) SEM, detail of helictoglossa;

(d) SEM, detail of intermissio;

(e) SEM, external valve face with central raphe endings (central pores).

in LM, and the clear difference in areola density and structure seen in SEM suggest that they are different taxa. Therefore it is concluded that *Encyonopsis* sp. A very likely represents an undescribed taxon, which may also be endemic. *Encyonopsis* sp. A was very common in the most acidic pools at Bealey (optimum pH 5.1).

***Encyonopsis* sp. B (Figure VI.9)**

Description of Bealey material: Valve very slightly dorsi-ventral, lanceolate, convex and slightly swollen at the centre so that the shape tends to rhombic. Narrow apices, slightly protracted (not capitate) and slightly curved to the ventral side. Length: 13.2 – 24.5 μm; breadth: 3.1 – 3.8 μm; striae: 28 – 30 per 10 μm, slightly radiate at the centre and parallel and sometimes slightly convergent at the apices. Raphe dorsally deflected at the centre, and at the apices strongly curved ventrally on the valve surface in a question-mark shape. Narrow axial area, widening to a definite central area. In SEM, the individual areolae making up the striae are round openings (about 40 per 10 μm); up to three of the central areolae closest to the central raphe endings on the dorsal side are enlarged into slits.

Comments: This small *Encyonopsis* species appears to have affinities with several other species, in particular the cosmopolitan taxon *E. microcephala* (Grunow) Krammer, which differs in shape and striae density but has similar dimensions and stria structure (Krammer 1997b) (Table VI.1). Other taxa found in the literature that resemble the Bealey taxon superficially are listed in Table VI.1. Of these, a species from Java, *E. thienemannii* (Hustedt) Krammer corresponds to the Bealey species most closely in dimensions but differs in the orientation of the striae (radial throughout in *E. thienemannii*), the shape of the axial area (linear, narrow with no central area) and in shape (more rounded sides in *E. thienemannii* as opposed to the rhombic shape of the Bealey populations). The other listed species all have more pronounced differences. No other similar species could be located in the available literature. It is therefore concluded that this species may represent a new and likely endemic taxon. *Encyonopsis* sp. B was relatively rare at Bealey. A very similar taxon has been noted from other locations in the South Island (data from Kilroy et al. 2007 [I]), but no SEM photographs are available for a detailed comparison.

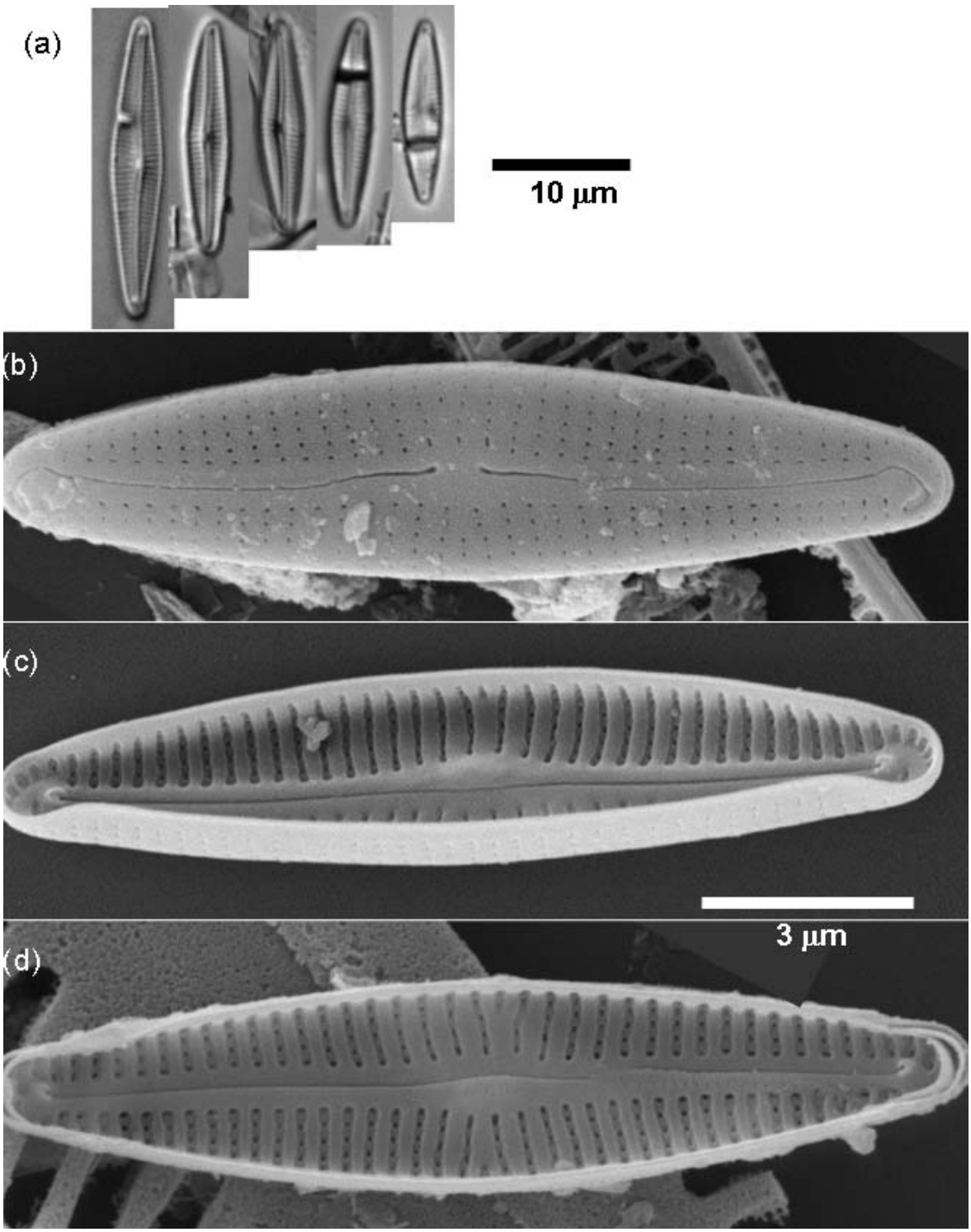


Figure VI.9. *Encyonopsis* sp. B. (a) LM, size declination; (b) SEM, external valve view; note the three slightly enlarged alveolae (stigmata) above the central raphe endings; (c) SEM, oblique internal view; (d) SEM, internal view.

Genus *Eunophora* Vyverman, Sabbe & Mann

The genus *Eunophora* was first described in 1998 from Tasmanian and New Zealand material (Vyverman et al. 1998). Currently three species are recognised, plus a fourth, *Amphora berggrenii* Cleve, which belongs in *Eunophora* but has yet to be formally transferred. *Eunophora* is very distinctive in that the valve faces are positioned side by side in the cell, as in *Amphora*, with very narrow or no girdle bands ventrally, and expanded bands dorsally. Whole cells normally lie so that both valves are visible more or less in valve view. In other respects, however, the genus is clearly closely related to *Eunotia* (Vyverman et al. 1998), including similar ecological requirements: both genera are found in dilute waters with low alkalinity. To date there have been no reports of *Eunophora* from any other regions. The genus is therefore assumed endemic to Australia (Tasmania) and New Zealand. At least some species could be described as "Flagship species": regional species that are so distinctive and showy that it is extremely unlikely that they would have been overlooked in other regions (Tyler 1996, Foissner 2006). Their presence in a restricted area is therefore taken as an indication that other less distinctive species in the same group of organisms could also be endemic to the same region. Two species of *Eunophora* were found in the Bealey samples. Both could be locally abundant, although they did not always co-occur.

Eunophora cf. *oberonica* (Figures VI.10, 11, 12)

Description of Bealey material: Cells solitary, strongly dorsi-ventral and elliptical to linear-elliptical when intact, 29 – 79 μm long, 20 – 24 μm wide. Four (or more?) chloroplasts (Figure VI.10). Individual valves dorsi-ventral, linear, with slightly concave dorsal and ventral margins and downpointing rounded apices, 8 – 9.5 μm wide. Striae cannot be resolved in LM except for a widely spaced area on the dorsal side: 16 – 18 per 10 μm. SEM counts show that stria density in the rest of the valve is up to about 36 per 10 μm. A sternum (hyaline area) lies ventral to the widely spaced striae, well-separated from the central raphe endings, but converging with the raphe towards the apices. The helictoglossae (internal silica thickenings at the raphe ends) are prominent in LM. Rimoportulae lie on the distal side of the raphe endings at approximately the same level. These are very obvious in LM if the valve is suitably orientated (Figure VI.11, arrowed). The valve surface is ornamented with a reticulum of silica ridges (looking like knitting) and the raphe is bordered by ribs (Figure VI.12a – d). Externally the ornamentation continues between and below the central raphe endings. Internally, there is a central unperforated region where the areolae (simple poroids) do not penetrate through to the interior (Figure VI.12f).

Comments: This taxon appears to be closely related to *E. oberonica*. However, both cells and valves are wider than those in Tasmanian populations (see Vyverman et al. 1998). In addition, the cells in LM show a consistently different outline: the apices are more sharply down-pointing rather than broadly rounded; in larger specimens the apices extend farther beyond the apical raphe

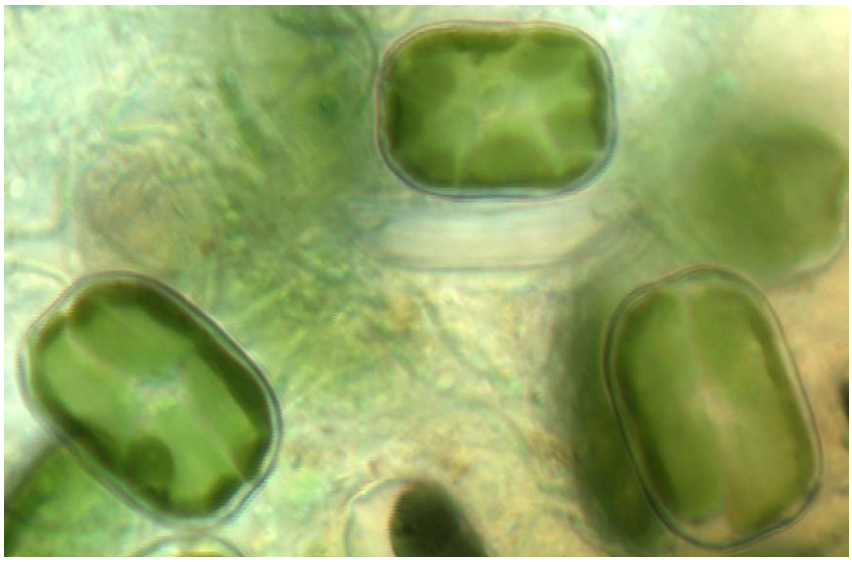


Figure VI.10
Eunophora cf. *oberonica*. Live cells photographed *in situ*, in association with fine cyanobaterial trichomes and cells within a microbial mat. The two lower cells apparently have four chloroplasts; the upper cell may have more.

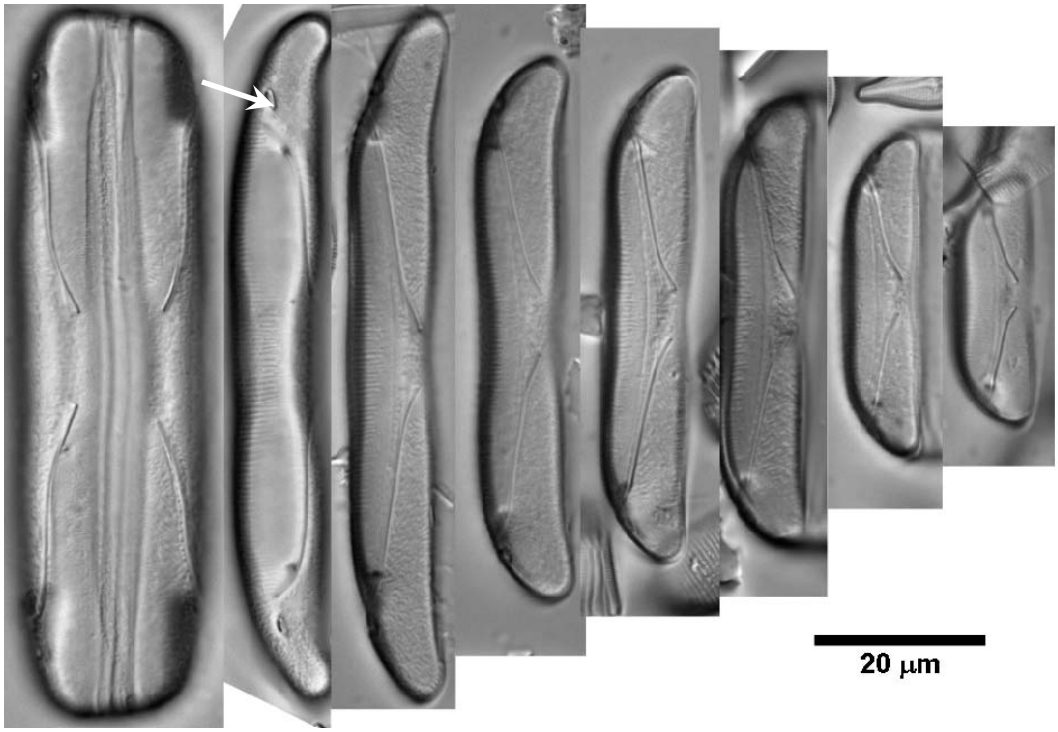


Figure VI.11 *Eunophora* cf. *oberonica*. LM, size declination, showing a whole frustule on the left. Arrow indicates rimoportula.

endings then in *E. oberonica*. In fact, in both dimensions and shape the Bealey populations more closely resemble *E. tasmanica*. However, they correspond with *E. oberonica* in (1) an abrupt change to more widely-spaced striae between the dorsal valve face and the mantle; and (2) fine structure (ornamented valve exterior) (Figure VI.12a – c). Thus, this species of *Eunophora* shares features with both *E. tasmanica* and *E. oberonica*, and likely represents a separate species. All three taxa possess rimoportulae (large openings to the interior of the valve) located between the distal raphe endings and the valve apices.

E. cf.. *oberonica* showed no clear optima for any water chemistry variable, including pH.

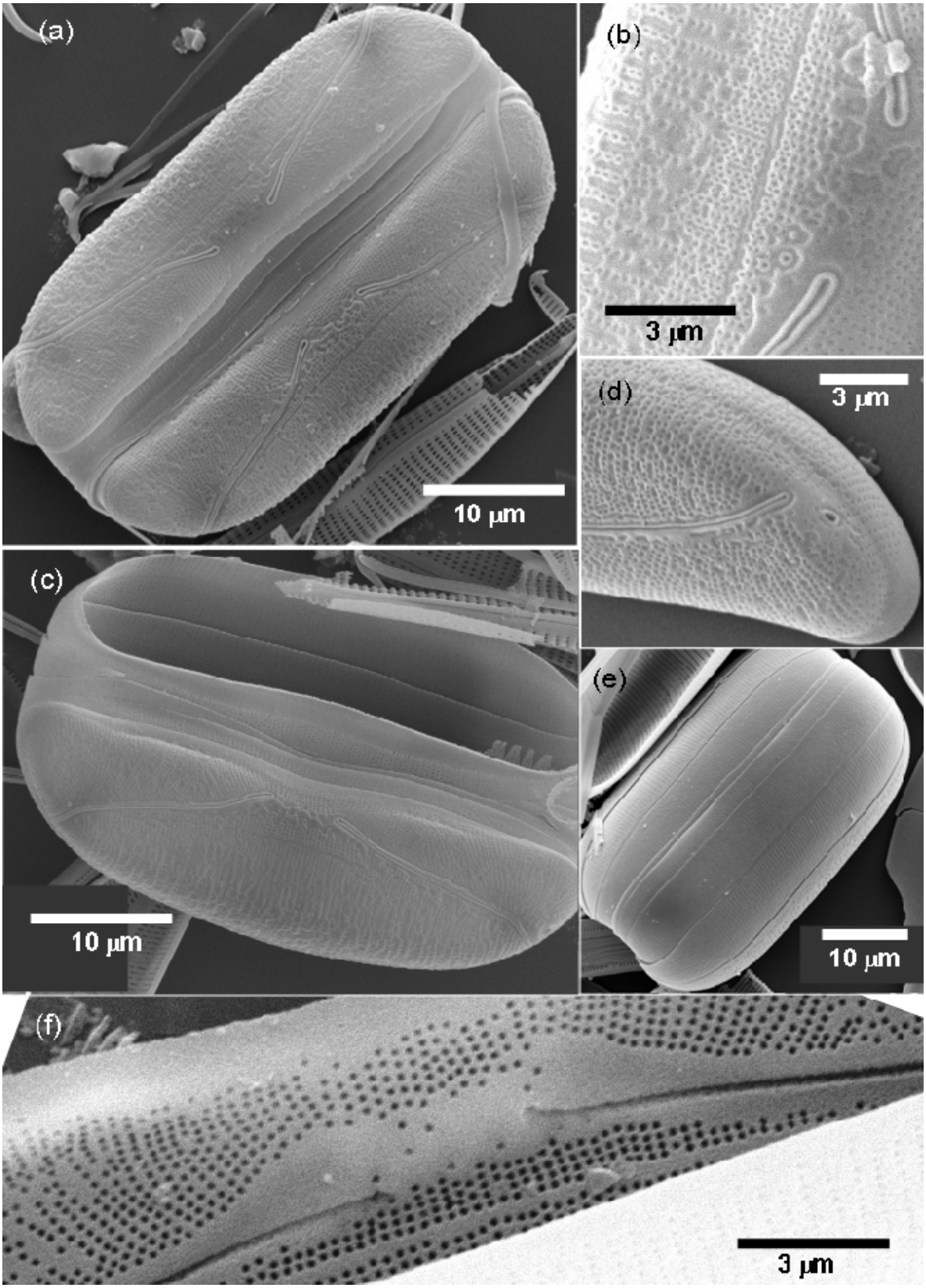


Figure VI.12 *Euophora* cf. *oberonica.* SEM. (a)Whole frustule, ventral view of both valve faces; (b) detail of central raphe endings and stria arrangement; (c) detail of internal and external girdle bands; (d) distal raphe ending showing rimoportula; (e) whole frustule, dorsal view (girdle bands); (f) detail of internal central raphe endings.

***Amphora berggrenii* Cleve (= *Eunophora* sp. 1 in Vyverman et al. 1998) (Figures VI.13, 14)**

Description of Bealey material: Cells solitary, strongly dorsi-ventral and elliptical to linear-elliptical when intact, 41.5 – 67 μm long, 27 – 29.5 μm wide. Multiple ribbon-like chloroplasts (Figure VI.13b). Individual valves dorsi-ventral, linear, with slightly concave dorsal and ventral margins and downpointing apices tapering to narrow rounded ends, 9 – 10 μm wide. Striae 15 – 16 per 10 μm, comprising rows of simple poroids, which are somewhat irregularly radiate and convergent below the raphe slits. Sternum (as in *E. oberonica*) visible on in occasional specimens. The area between the central raphe ending is free of striae. Helictoglossae prominent in LM but rimoportulae absent.

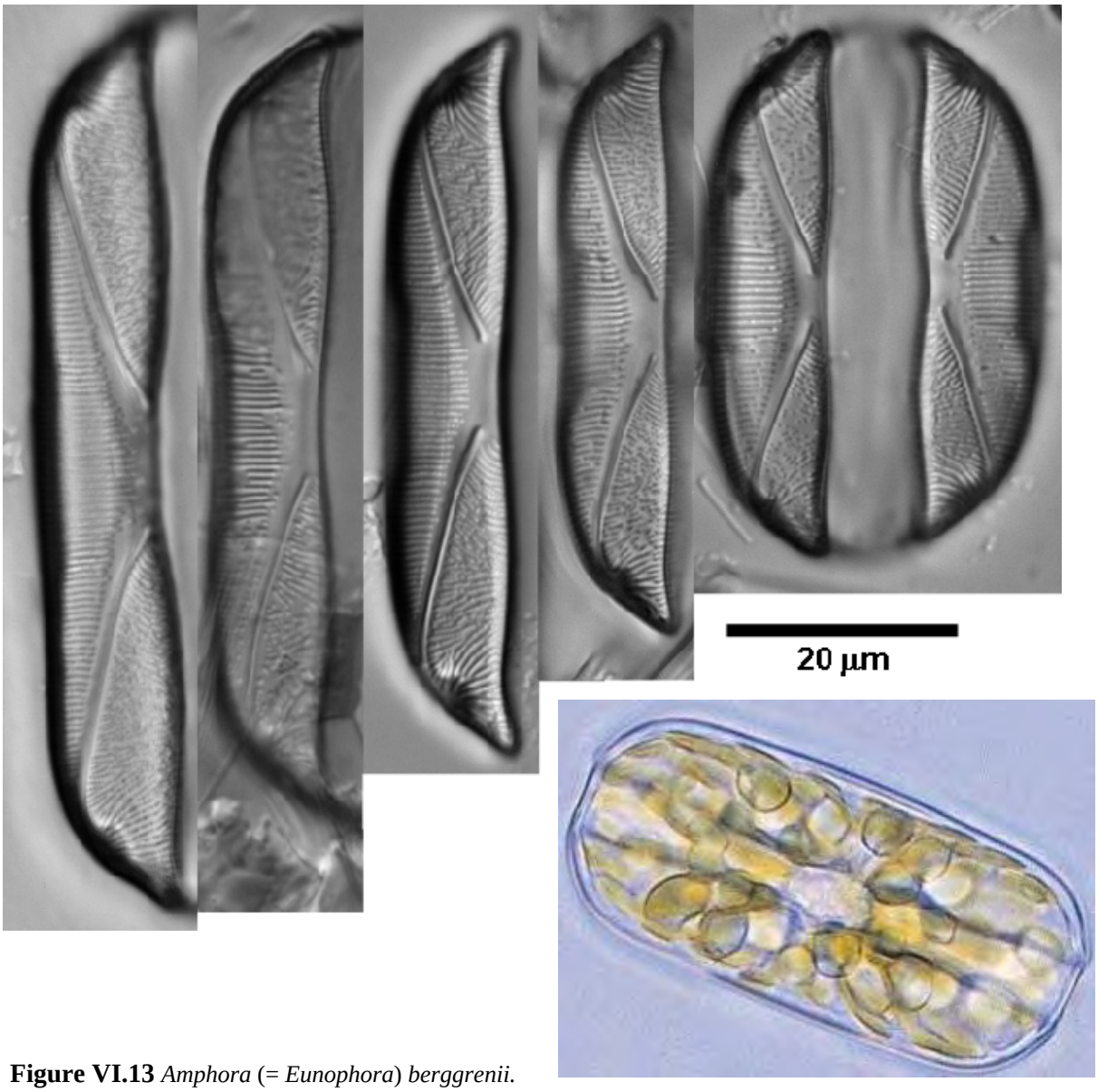


Figure VI.13 *Amphora* (= *Eunophora*) *berggrenii*. (a) LM, size declination; (b)LM, live cell showing radiating ribbon-like chloroplasts.

Comments: The original report of this taxon included two line drawings (Cleve 1881), which correspond to the taxon at Bealey. Interestingly, the species was initially described from fossil material from Arthurs Pass, New Zealand. The exact location is unknown. Vyverman et al. (1998) discussed populations of this taxon in Tasmania, which appear very similar to the Bealey material. To my knowledge the species has not yet been formally transferred to *Eunophora*.

Amphora (E.) berggrenii showed no clear optima for any water chemistry variable, including pH.

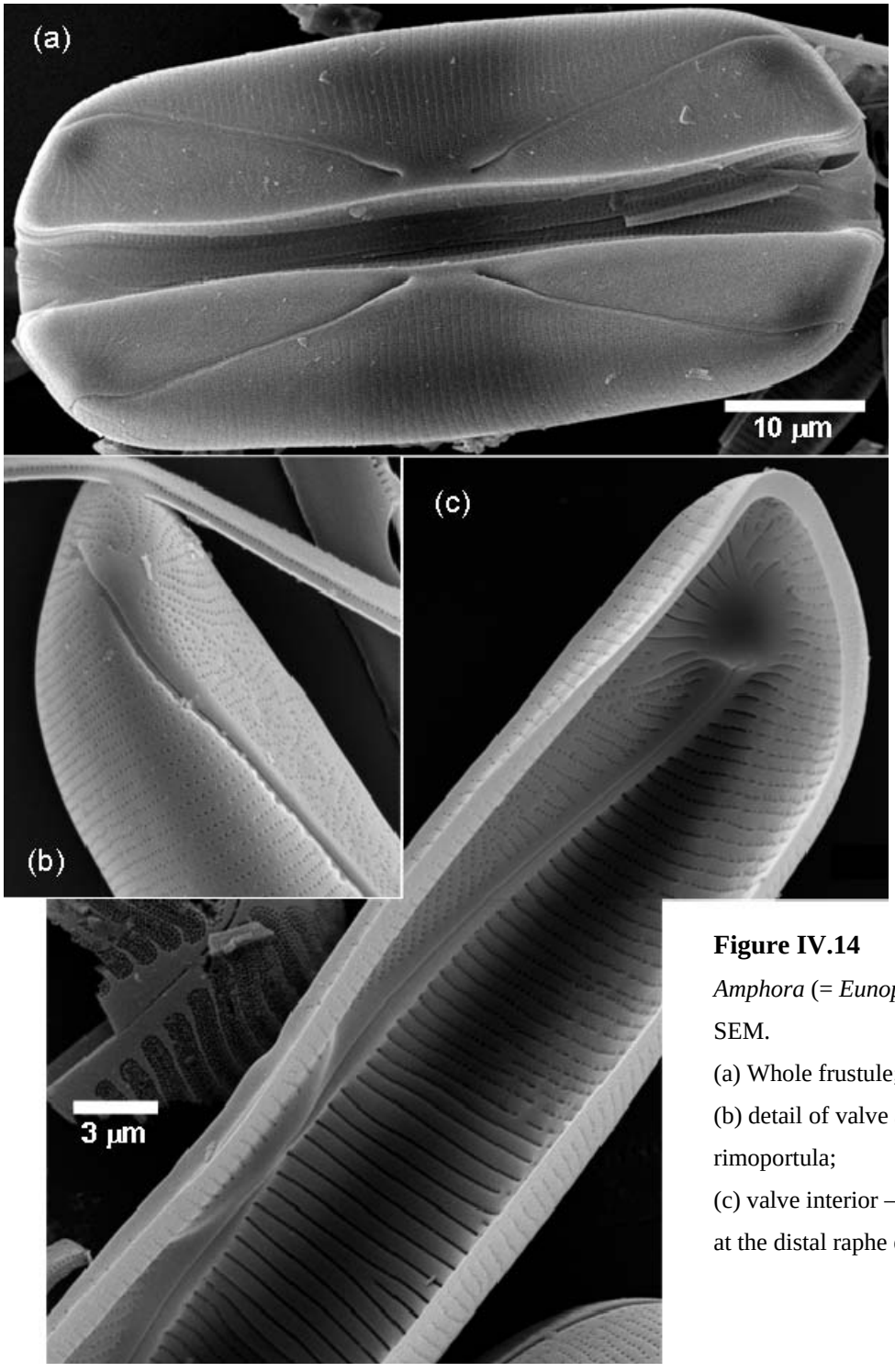


Figure IV.14
Amphora (= *Eunophora*) *berggrenii*, SEM.
(a) Whole frustule;
(b) detail of valve apex – note lack of rimoportula;
(c) valve interior – note helictoglossa at the distal raphe ending.

Genus *Eunotia Ehrenberg*

The genus *Eunotia* is defined by possession of short raphe slits positioned to the side of the valve and not coincident with the sternum (Round et al. 1990). Most species in this large genus are confined to oligotrophic / dystrophic acidic waters with low conductivity. Round et al. (1990) considered *Eunotia* to be "in need of revision at the species level". Krammer and Lange-Bertalot (1991) provided accounts of 52 species with numerous varieties and acknowledged their great morphological variability. Since the early 1990s many further species have been described or recognised (e.g., Lange-Bertalot and Metzeltin 1996, Metzeltin and Lange-Bertalot 1998, Rumrich et al. 2000). At Bealey, numerous different forms of *Eunotia* were recognised, most of which were rare. One taxon recurred in many pools.

***Eunotia bilunaris* var. *mucophila* Lange-Bertalot & Norpel (Figure VI.15)**

Description of Bealey material: Cells long, very narrow, slightly curved with ends very slightly deflected dorsally (most noticeable in larger specimens), 36 – 80 μm long, 1.8 – 2.6 μm wide. Striae parallel throughout 20 – 24 per 10 μm, composed of simple poroids. Terminal nodules (helictoglossae) visible in LM. Internally, in SEM a single rimoportula present at one end adjacent to the terminal nodule (not illustrated), and a break in the striae underlying the external raphe slit (Figure VI.15b, arrowed).

Comments: The dimensions, shape and internal structure of the Bealey specimens precisely correspond to the description and illustrations of European populations of *E. bilunaris* var. *mucophila* in Krammer and Lange-Bertalot (1991). New Zealand (including Bealey) and Tasmanian populations of this taxon have been shown to be capable of interbreeding and therefore are conspecific (Vanormelingen et al. 2007). Molecular data also suggested relatively recent interchange of these diatoms across the Tasman Sea. However, these authors state that "it would be premature to conclude that the European material described previously as *mucophila* and our Australasian *bilunaris* belong to the same species". Despite this doubt, and in the absence of a similar comparison between European and Australasian material, for the present analysis I assume that morphological correspondence with European populations (as there was between the New Zealand and Tasmanian populations) indicates that this is a cosmopolitan taxon.
E. bilunaris var. *mucophila* was very common in some pools (>12% numerically) and showed a definite preference for lower pH values.

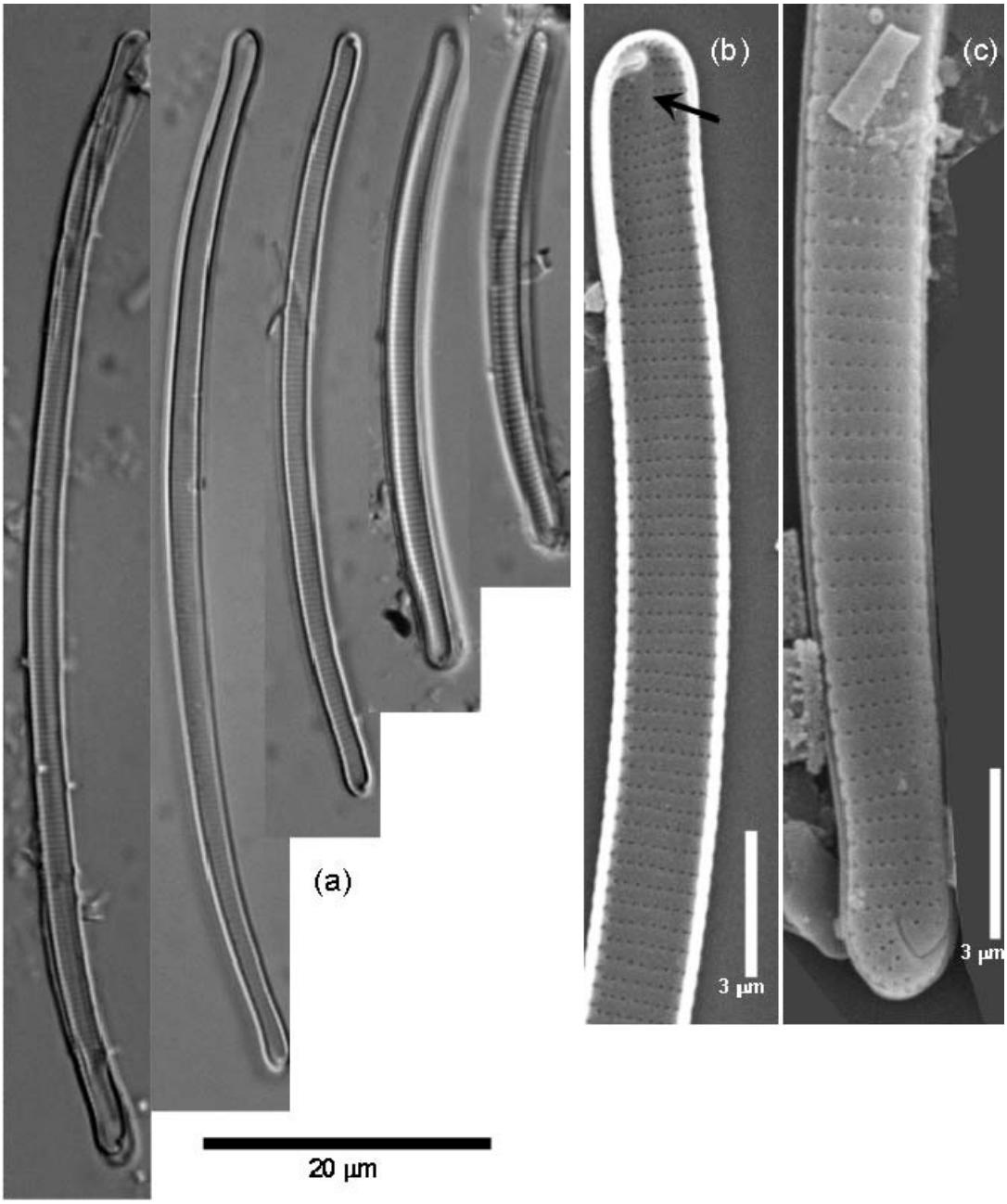


Figure VI.15 *Eunotia bilunaris* var. *mucophila*. (a) LM, size declination; (b) SEM, internal view – note break in striae (arrowed); (c) external view.

Genus *Frustulia* Rabenhorst

In common with *Brachysira*, *Eunotia* and other taxa, the genus *Frustulia* is typically found in oligotrophic, acidic waters, particularly in peat bogs (e.g., Siver and Baskette 2004). The genus has well-defined characters (see Round et al. 1990) and can be extremely common (e.g., Gaiser and Johansen 2000). At Bealey, *Frustulia* was the second most common genus after *Brachysira* (Kilroy et al. 2006 [II]) and four species were relatively common.

***Frustulia saxonica* Rabenhorst (Figures VI.16, 17)**

Description of Bealey material: valves broad, rhombic with narrow, rounded and slightly protracted ends. Length: 63 – 96 μm, breadth 15 – 20.5 μm, striae approx. 28 – 38, parallel throughout the valve. About 30 – 31 areolae per 10 μm (counted as parallel lines along the apical axis), consistent throughout the valve. Raphe straight. At the apices the raphe canal ends in more or less triangular nodules, with striae visible right around the tips (clearly seen in SEM, Figure VI.17d). Externally the raphe ends with a T-shape (Figure VI.17a,b).

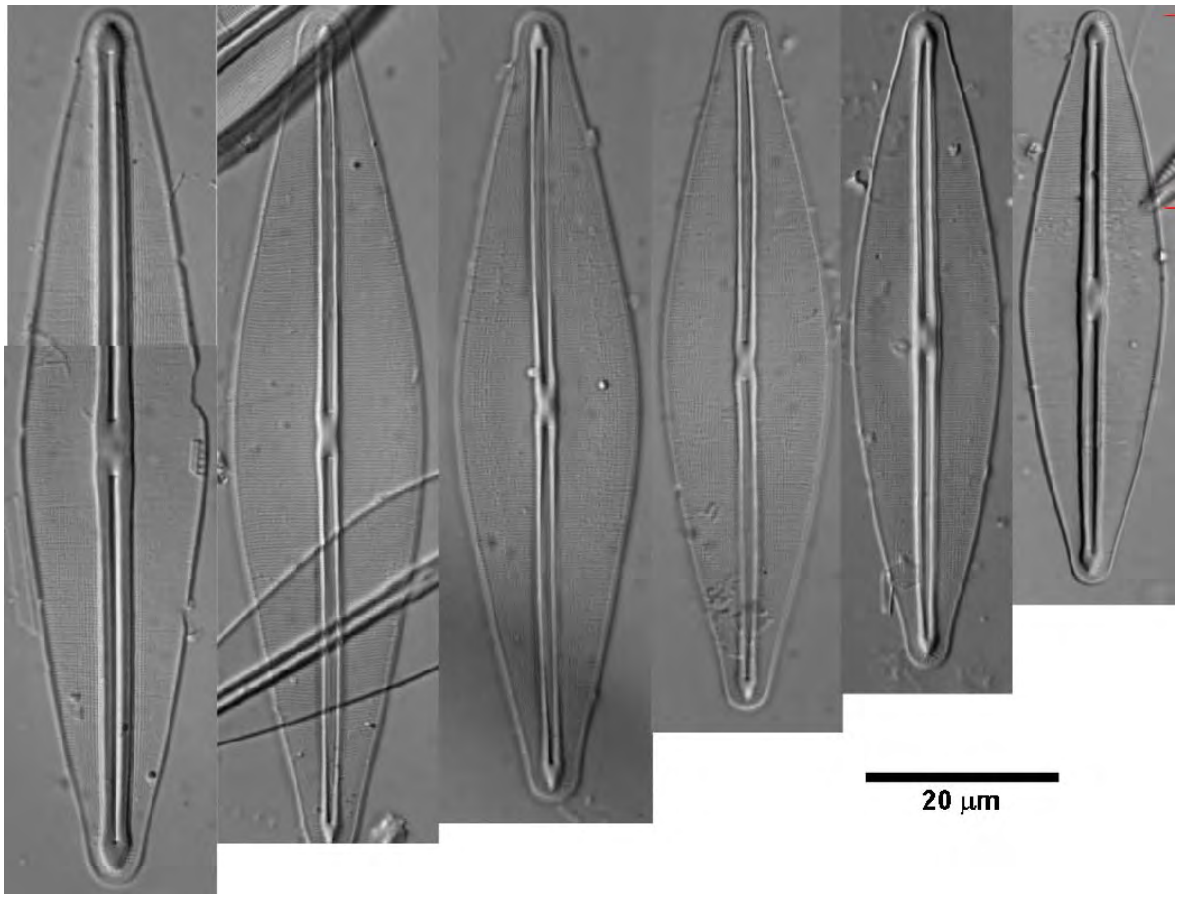


Figure VI.16 *Frustulia saxonica*, LM, size declination. Note the broader raphe area in the left-hand valve, resulting from different focussing.

Comments: This species was named *Frustulia rhomboides* (Ehrenberg) De Toni in Kilroy et al. (2006 [II]). Note that *F. rhomboides* has now been transferred to *F. krammeri* Lange-Bertalot because of misinterpretation of the type specimen of *Navicula rhomboides* Ehrenberg (Lange-Bertalot and Jahn 2000). The distinction between *F. krammeri* and *F. saxonica* was discussed in detail in Lange-Bertalot (2001) and more recently by Siver and Baskette (2004), and is still debatable. However, the populations at Bealey are entirely consistent with *F. saxonica* as described by Lange-Bertalot (2001). The fine structure is also consistent with the description in Siver and

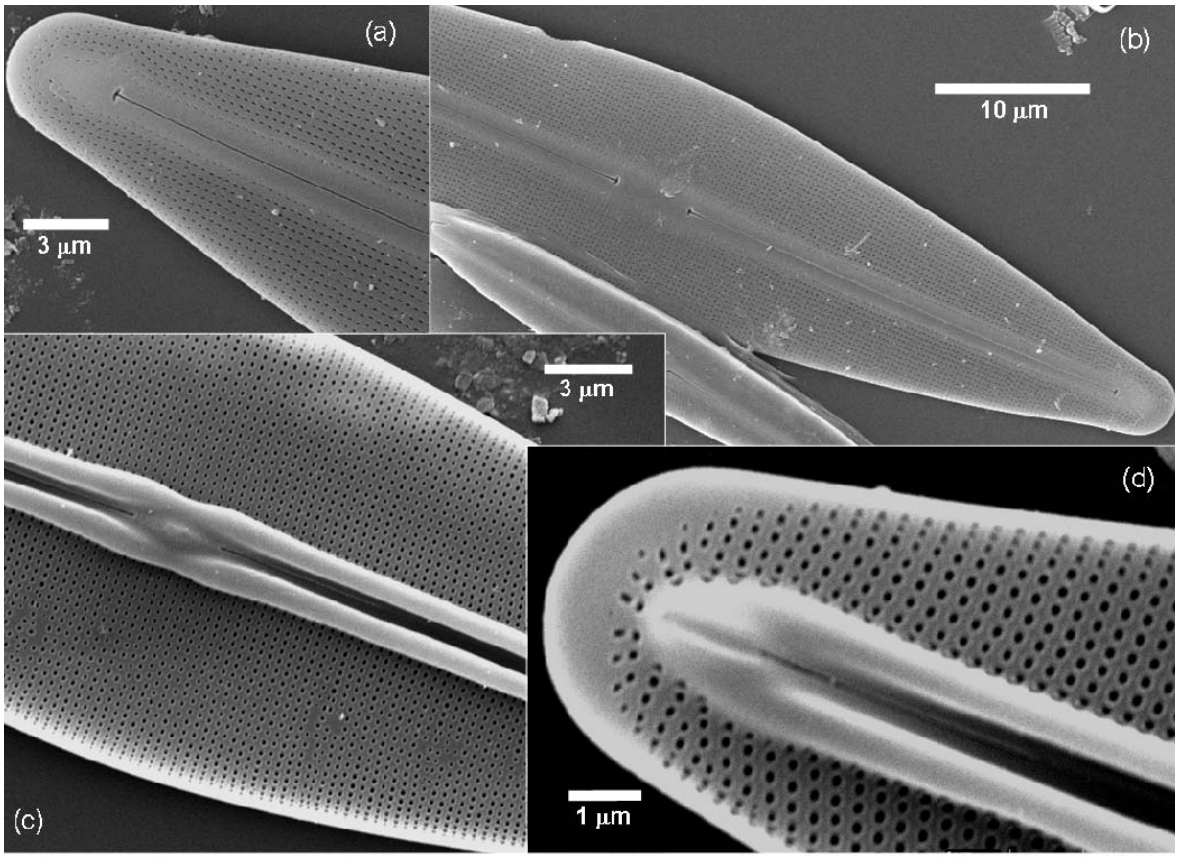


Figure VI.17 *Frustulia saxonica*, SEM. (a) External view of valve end; (b) external valve view; (c) internal view, central nodule; (d) linear helictoglossa.

Baskette (2004). In particular, the raphe-canal endings in the Bealey specimens match those described for *F. saxonica*, rather than those for *F. krammeri*, which are more elongated. Beier and Lange-Bertalot (2007) illustrated specimens from West Coast lowland wetlands, which also correspond with *F. saxonica*. *F. saxonica* has been reported from acid, low alkalinity waters worldwide (Lange-Bertalot 2001).

***Frustulia* sp A. (Figures VI.18, 19)**

Description of Bealey material: valves lanceolate with rostrate, protracted apices and smooth convex margins. Internal undulations (often not evident in SEM) result from curved internal projections from the girdle bands. Length: 47.5 – 66 μm, breadth 9.3 – 11.6 μm, striae (counted in SEM) 34 per 10 μm, absent within a central area of variable size, approximately 1.5 – 2 μm broad and spanning up to three quarters of the valve width (usually less). A single row of areolae continues through the central area adjacent to the central raphe endings. Raphe endings T-shaped and similar to those in *F. crassinervia* (Brebisson) Lange-Bertalot & Krammer (Siver and Baskette 2004).

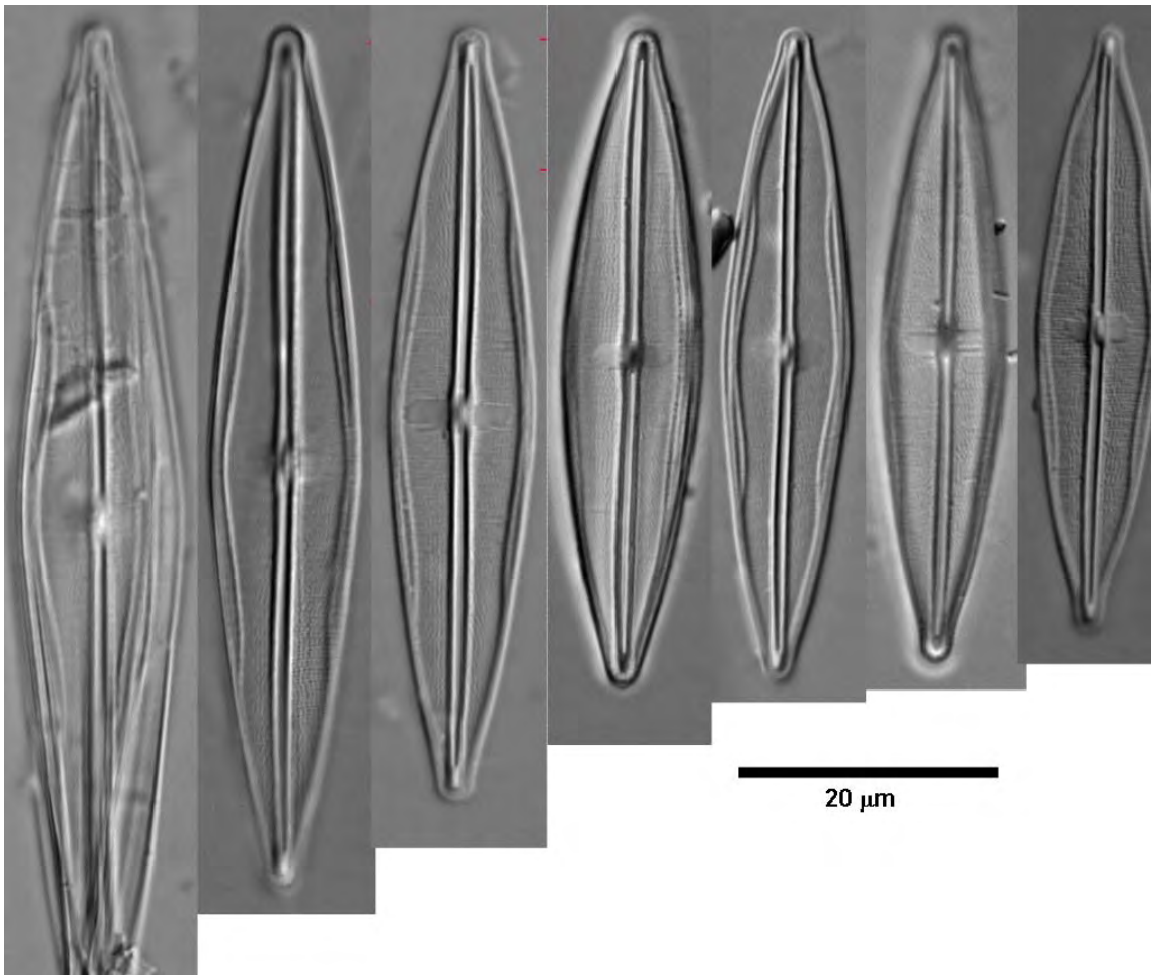


Figure VI.18 *Frustulia* sp. A, LM, size declination.

Comments: The main distinguishing feature of this taxon is its areolae-free central area. In this respect, and in general outline, *Frustulia* sp. A from Bealey species resembles *F. pseudoundosa* Flower, which was described from Adam Tarn in the Falkland Islands (Flower 2005). *F.* sp. A differs from *F. pseudoundosa* in its longer length (non-overlapping length range), coarser striation (Table VI.1) and in outline details. *F. pseudoundosa* has undulating margins, while those of *F.* sp. A are smooth; the former species usually shows distinctly capitate apices, while those of *F.* sp. A are protracted but not capitate. The internal undulations of the girdle bands in *F.* sp. A are observed in other species, e.g., *Frustulia nana* Moser, Lange-Bertalot & Metzeltin (Moser et al. 1998). *Frustulia* sp. A was the second most common species of *Frustulia* found at Bealey, and occurred mostly in pools with higher pH (Kilroy et al. 2006 [II]). This distinctive species has been observed in samples from other mire pool / tarn habitats in New Zealand (Kilroy et al. 2007 [I]). The presence of a clear central area in *Frustulia* has thus far only been observed in species from the Southern Hemisphere (Rumrich et al. 2000, Van der Vijver 2002, Flower 2005). It is therefore reasonable to assume that our *Frustulia* sp. A represents an exclusively Southern Hemisphere taxon, and very likely a species endemic to New Zealand.

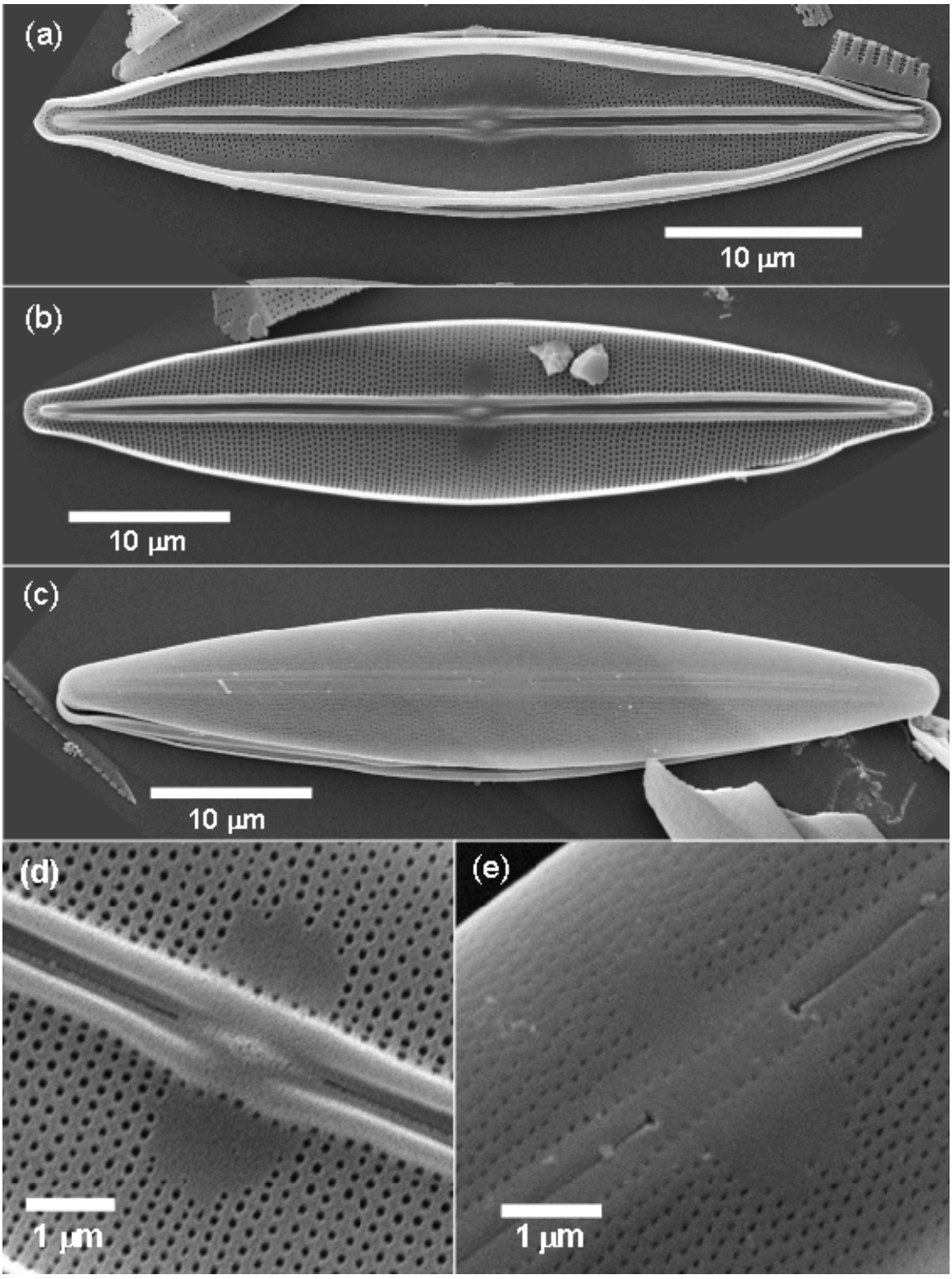


Figure VI.19 *Frustulia* sp. A, SEM. (a) internal valve view, with one girdle band in place, showing silica projections that give the valve the "wavy" internal outline seen in LM (Figure VI.18); (b) internal valve view – note hooped helictoglossae at the apices; (c) external valve view; (d) central nodule and internal appearance of areolae-free area; (e) detail of external central raphe endings.

***Frustulia* cf. *magaliesmontana* Cholnoky (Figure VI.20)**

Description of Bealey material: valves narrow lanceolate with curved sides and protracted ends, often slightly capitate. tending to elongated rhombic, tapering to narrowly rounded ends which are not at all protracted. Length: 51 – 62 μm, breadth 7.9 – 8.7 μm, transapical striae hard to resolve in LM, approx. 39 per 10 μm, parallel in the centre and becoming convergent towards the poles. About 37 – 38 areolae per 10 μm (counted as parallel lines along the apical axis. or apical striae). Raphe straight, terminating both centrally with and distally with a barely differentiated pore. There is a gap in the striae at the apices (Figure VI.20c).

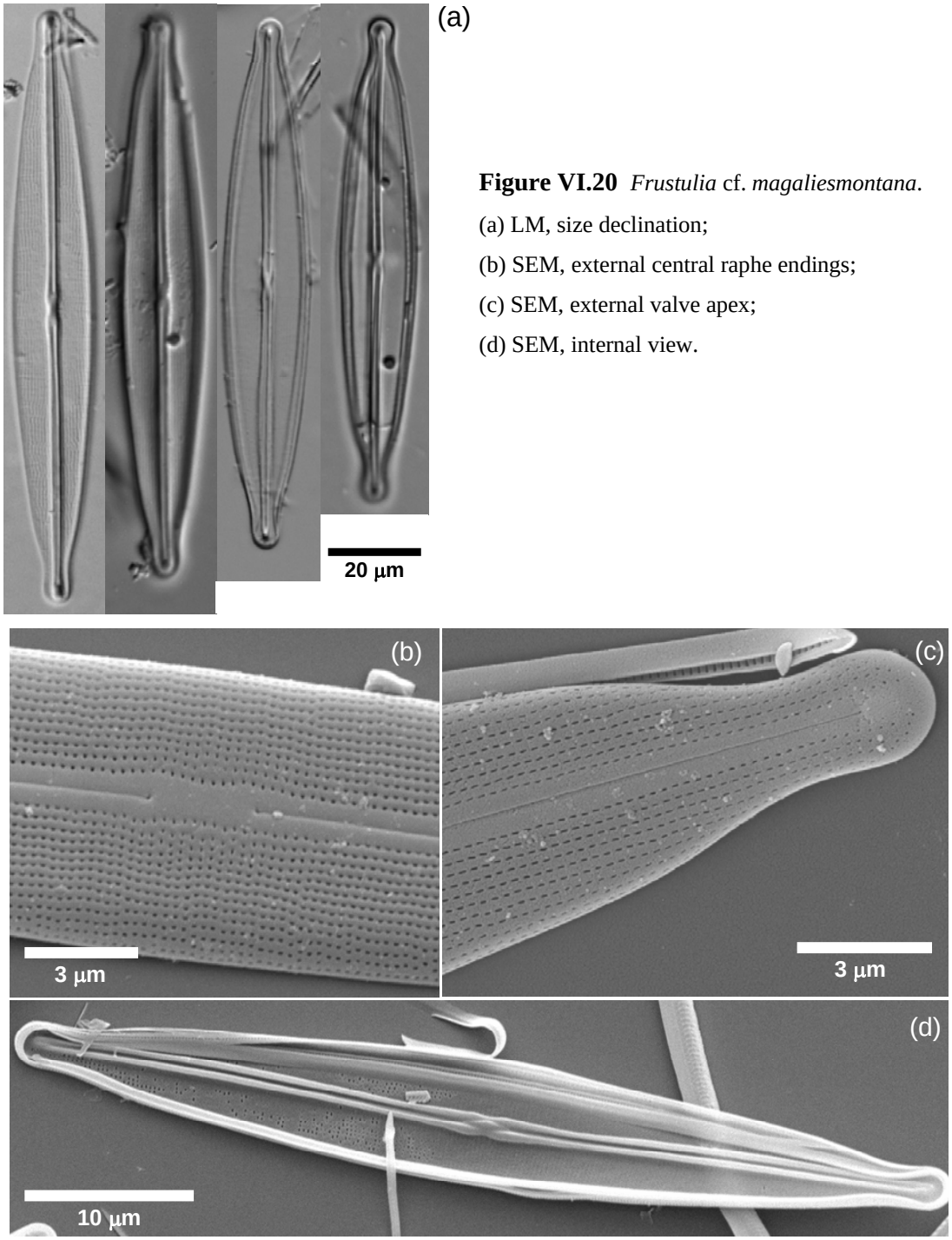


Figure VI.20 *Frustulia* cf. *magaliesmontana*.
(a) LM, size declination;
(b) SEM, external central raphe endings;
(c) SEM, external valve apex;
(d) SEM, internal view.

Comments: This species was identified as the cosmopolitan species, *F. magaliesmontana* Cholnoky, in Kilroy et al. (2006 [II]). *F. magaliesmontana* was described from South Africa and a similar species was reported from Canada (Fallu et al. 2000). Beier and Lange-Bertalot (2005) discussed *F. magaliesmontana* in detail in relation to populations similar to those at Bealey, found in lowland wetlands on the West Coast, South Island, New Zealand. These populations are similar to specimens from North Island (Foged 1979) and Eastern Australia (Foged 1978) but differ in outline from the type material of *F. magaliesmontana*, which has parallel sides (Beier and Lange-Bertalot 2007, Figs 8 –10). The Canadian taxon has been described as a new species, *F. pseudomagaliesmontana* Camburn & Charles (see Siver and Baskette 2004 for a detailed description), which differs from the New Zealand / Australian populations mainly in its smaller size range. In fine structure – particularly the raphe endings – the populations from South Africa and New Zealand are remarkably similar (compare SEMs in Moser et al. 1995, Pl. 36, 37, and Beier and Lange-Bertalot 2007, Figs. 4.44 – 4.49, with those below). *F. pseudomagaliesmontana* also shares the same features (Siver and Baskette 1995, Figs 60, 64). Given the variation in dimensions and stria counts in all these populations it is difficult to draw any conclusions about conspecificity, as discussed by Beier and Lange-Bertalot (2007).

***Frustulia cassieae* Lange-Bertalot & Beier (Figure VI.21)**

Description of Bealey material: valves narrow lanceolate tending to elongated rhombic, tapering to narrowly rounded ends which are not at all protracted. Length: 80 – 113 μm, breadth 11 - 14 μm, striae approx. 29 – 31, parallel in the centre and becoming slightly convergent towards the poles. About 30 – 31 areolae per 10 μm (counted as parallel lines along the apical axis), with slightly wider and more irregular spacing at the centre of the valve. Raphe straight. Two isolated pores are present in the central area, visible in LM with careful focusing (see Figure VI.21). At the apices the raphe ends in more or less triangular nodules, with striae visible right around the tips.

Comments: This species was identified in Kilroy et al. (2006 [II]) as *Frustulia rhomboides* var. *elongatissima* Manguin (now transferred to *F. elongatissima* Lange-Bertalot) from illustrations in Foged (1978, 1979). However, the Bealey specimens under LM conform precisely to *F. cassieae*, which has been recently described as a new species from material collected in "slightly acidic, minerotrophic swamps" on the West Coast, South Island, New Zealand (Beier and Lange-Bertalot 2007). These authors also differentiated this new species from the similar *F. blancheana* (see Table VI.1). Unfortunately no Bealey specimens have yet been located under SEM. This taxon occurred in the less acidic pools at Bealey and was rare in all but two. *F. cassieae* has been synonomised with Foged's *F. rhomboides* var. *elongatissima* specimens from both North Island and Eastern Australia, presumably on the basis of their slightly smaller size compared to the original *F.*

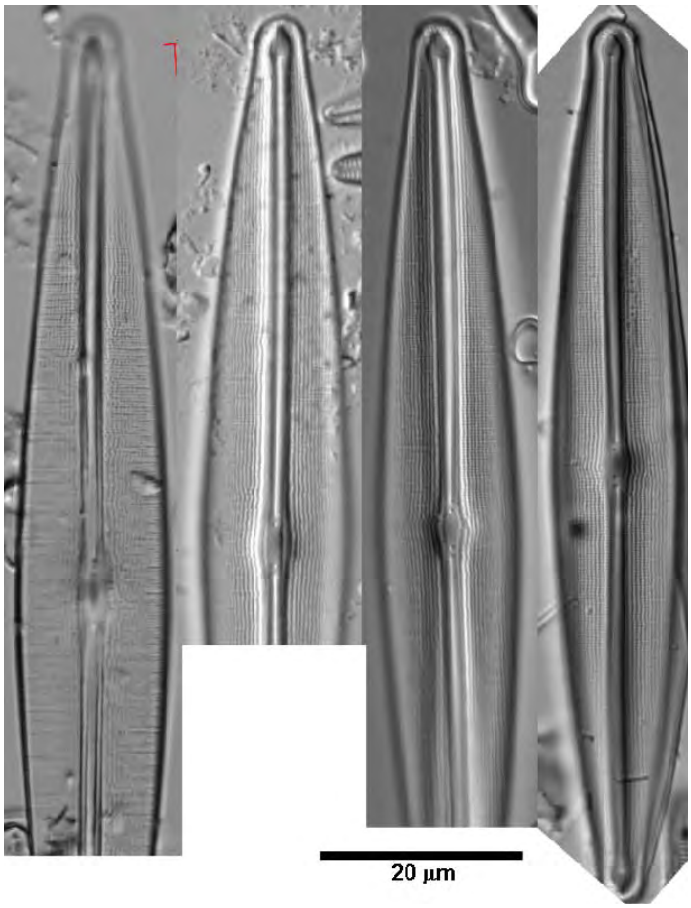


Figure VI.21
Frustulia cassieae, LM.

elongatissima. The distinctive central pores are not evident in Foged's illustrations. Small specimens identified as *F. elongatissima*, and which closely resemble the present species, have also been found in Tasmanian mountain lakes (Vyverman et al. 1995). This suggests a possible New Zealand / eastern Australia / Tasmania distribution for this species indicating that it is likely to be endemic to this region rather than to New Zealand alone.

Genus *Kobayasiella*

Kobayasiella was erected to encompass a distinctive group of taxa formerly included in *Navicula* (Lange-Bertalot 1996, 1999)[2]. Vanhoutte et al. (2004) provided a comprehensive description of generic features and described four new species of *Kobayasiella* from highland lakes in Tasmania. These authors also listed all 19 species of *Kobayasiella* known at the time of writing (including the four new species). At least three species of *Kobayasiella* were common in the samples from Bealey and I have compared the morphological characteristics of these species with those of the 19 species listed by Vanhoutte et al. (2004). I conclude that two of the species at Bealey are likely to be new and endemic, and the third is indistinguishable from a known Northern Hemipshere taxon.

[2] This genus was initially named *Kobayasia* (Lange-Bertalot 1996), but all species were transferred to *Kobayasiella* (Lange-Bertalot 1999) after it was realized that the name *Kobayasia* was already in use.

***Kobayasiella* sp. A (Figure VI.22)**

Description of Bealey material: Valves lanceolate to elliptical, with rostrate or barely capitate apices. Length: 23 – 41 µm, breadth 5.5 – 6.3 µm, striae 38 – 39 per 10 µm at the centre of the valve. Striae convergent at the centre of the valve, becoming abruptly divergent near the poles (this is diagnostic for all *Kobayasiella* species). Each striae comprises a single elongated areola. Narrow axial area, often broadening to a rhombic shaped central area, which is much more pronounced in large than in small specimens. The central raphe endings are slightly widened. At the apices, the outer raphe endings are strongly hooked.

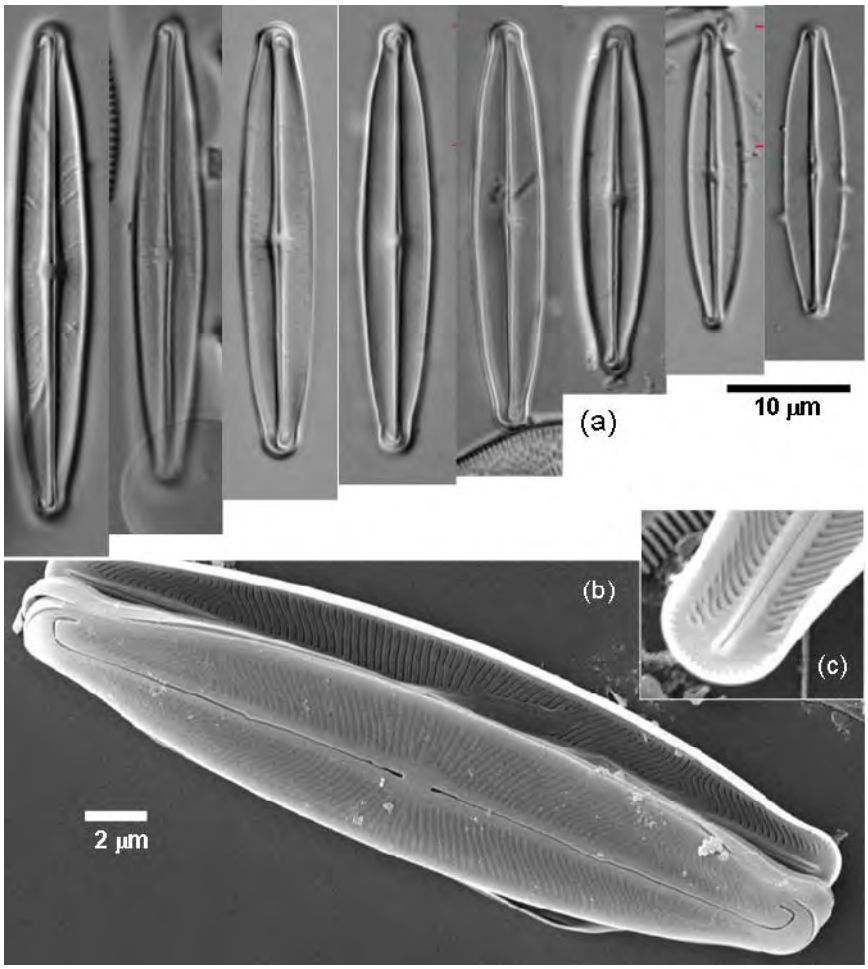


Figure VI.22
Kobayasiella sp. A.
(a) LM, size declination;
(b) SEM, external valve view (note internal view behind);
(c) detail of internal distal raphe ending.

Comments: This species is most similar to *K. acidophila* Vanhoutte, described from Tasmania. The species have similar stria fine structure, but *K.* sp. A has larger dimensions (non-overlapping width). Both *K. acidophila* and *K.* sp. A differ from the very common Northern Hemisphere species *K. subtilissima* in the fine structure of the striae and in their elliptical rather than linear shape (see Vanhoutte et al. 2004). For these reasons it is assumed that there is a high probability that K. sp. A represents a taxon that is endemic to New Zealand.

Kobayasiella sp. A was common throughout the Bealey wetland with a slight tendency to be more abundant in the less acidic sites.

***Kobayasiella* sp. B (Figure VI.23)**

Description of Bealey material: Valves elliptical, with capitate apices. Length: 44 – 47.5 μm, breadth 7.7 – 8.4 μm, striae 39 per 10 μm at the centre of the valve. Striae convergent at the centre of the valve, becoming abruptly divergent near the poles (this is diagnostic for all *Kobayasiella* species). Each striae comprises a single elongated areola. Narrow axial area, usually broadening to a distinctly rhombic central area. The central raphe endings are very slightly expanded. At the apices, the outer raphe endings are strongly hooked.

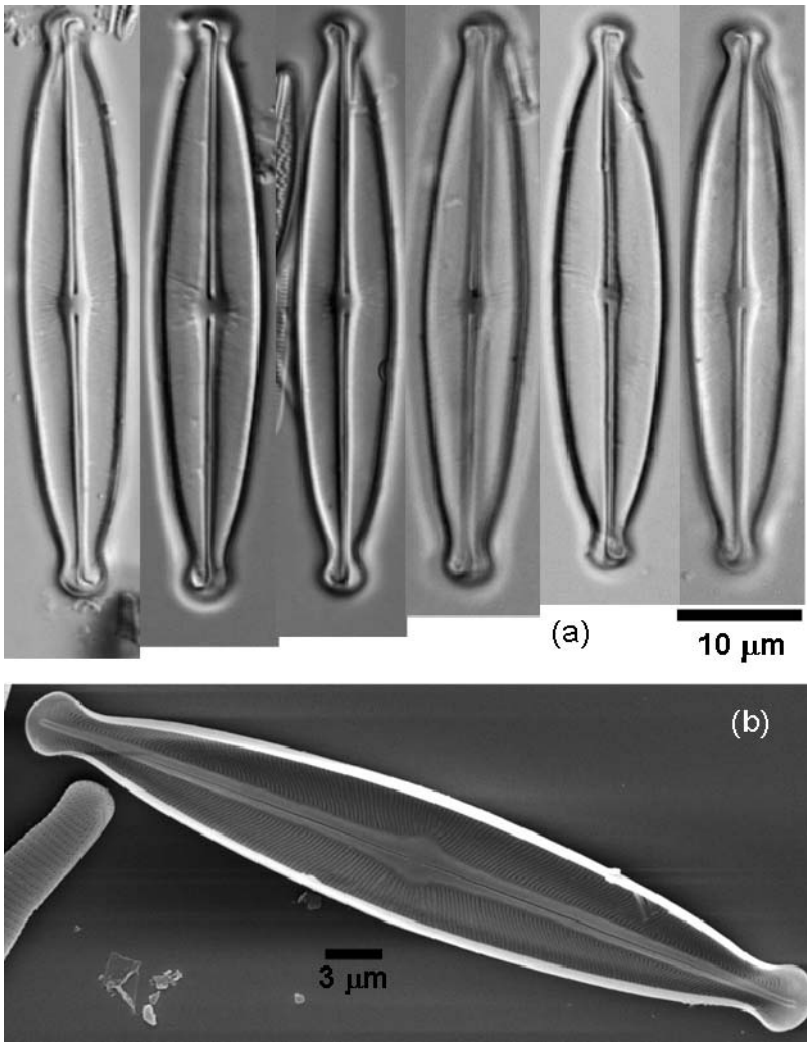


Figure VI.23
Kobayasiella sp. B.
(a) LM, note little size variation documented to date;
(b) SEM, internal view.

Comments: This species resembles *K. madumensis* (Jorgensen) Lange-Bertalot (from Europe) and *K. krasskei* (Metzeltin and Lange-Bertalot) Lange-Bertalot (from South America), but is consistently larger than *K. madumensis*, in both length and width. It is similar in length to *K. krasskei*, but consistently narrower, and also has markedly capitate apices as opposed to the definitely rostrate ends in *K. krasskei*. Stria density is also greater than in *K. krasskei*, which has only 27 – 28 striae/10 μm (Metzeltin and Lange-Bertalot 1998). At Bealey, the species was clearly differentiated from *Kobayasiella* sp. 1 by its larger size and distinctly capitate apices. *Kobayasiella* sp. B occurred only in pools with pH < 6. Since this species is large, relatively distinctive and could

be relatively common (>7% of the community), yet has not been encountered elsewhere, it is assumed that there is a high chance that *Kobayasiella* sp. B is endemic to New Zealand.

***Kobayasiella parasubtilissima* (Kobayasi & Nagumo) Lange-Bertalot (Figure VI.24)**

Description of Bealey material: Valves linear with a slightly convex margin and with capitate apices. Length: 22 – 24 µm, breadth 3.8 µm, striae not visible under LM. Narrow axial area, usually broadening to a distinctly rhombic central area. Axial area narrow with a small rounded central area. Terminal endings bent (hooked). No marked expansion of the central raphe endings visible in LM.

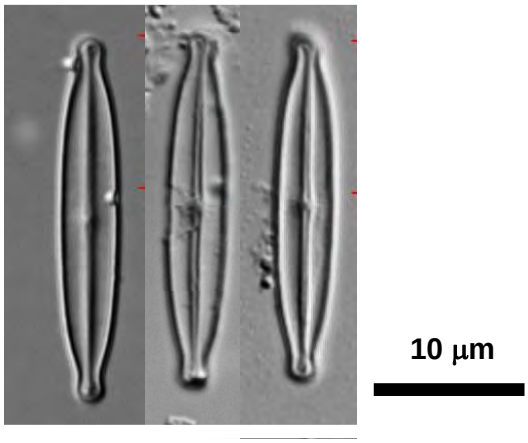


Figure VI.24.
Kobayasiella parasubtilissima, LM.

Comments: The shape, dimensions and LM-visible features of this species were consistent with *K. parasubtilissima*, but with no other known species of *Kobayasiella*. Although easily distinguishable in LM from other *Kobayasiella* species at Bealey, this small species was relatively uncommon at all sites (maximum 2.4% by cell number) and no specimens have been located under SEM to date. At this stage this species is assigned to *K. parasubtilissima*, which has been recorded from throughout the Northern Hemisphere, including the Pacific region (Japan) (Vanhoutte et al. 2004).

Genus *Navicula* Bory

This extremely common genus is characterized mainly by its bilaterally symmetrical, spindle-shaped ("naviculoid") outline. Because many diatoms share this feature *Navicula* has tended to be a catch-all for species in which other defining characteristics are unclear (Round et al. 1990). Obvious groups such as *Pinnularia* and *Neidium* have long been separated from *Navicula*; less obvious groups such as *Craticula*, *Geissleria* and *Adlafia* (among others, Lange-Bertalot 2001) have been separated more recently. At least one genus (*Placoneis*) has been separated from *Navicula* on the basis of chloroplast structure (Cox 1987). Nevertheless, *Navicula*, as defined by its type species, has a distinctive set of characteristics (Cox 1979), and variation within the genus has been documented in detail (Cox 1999). Two species at Bealey were placed in this genus and neither was particularly common. The most widespread is described here.

***Navicula* sp. A (Figure VI.25)**

Description of specimens from Bealey: Valves naviculoid tapering smoothly to narrow, almost pointed, apices. Length: 42 – 52 μm, breadth 9 – 10 μm, striae 10 - 13 in 10 μm. Narrow axial area widening to a prominent round central area occupying almost half of the valve width. Central raphe endings strongly curved towards the primary side of the valve (the side without the Voigt fault, Cox 1999), terminating in a rounded hook shape. Distal raphe ends hooked over the valve apex in the same as the central raphe endings. Striae punctuate, radiate at the centre of the valve, becoming parallel or (barely) divergent towards the apices.

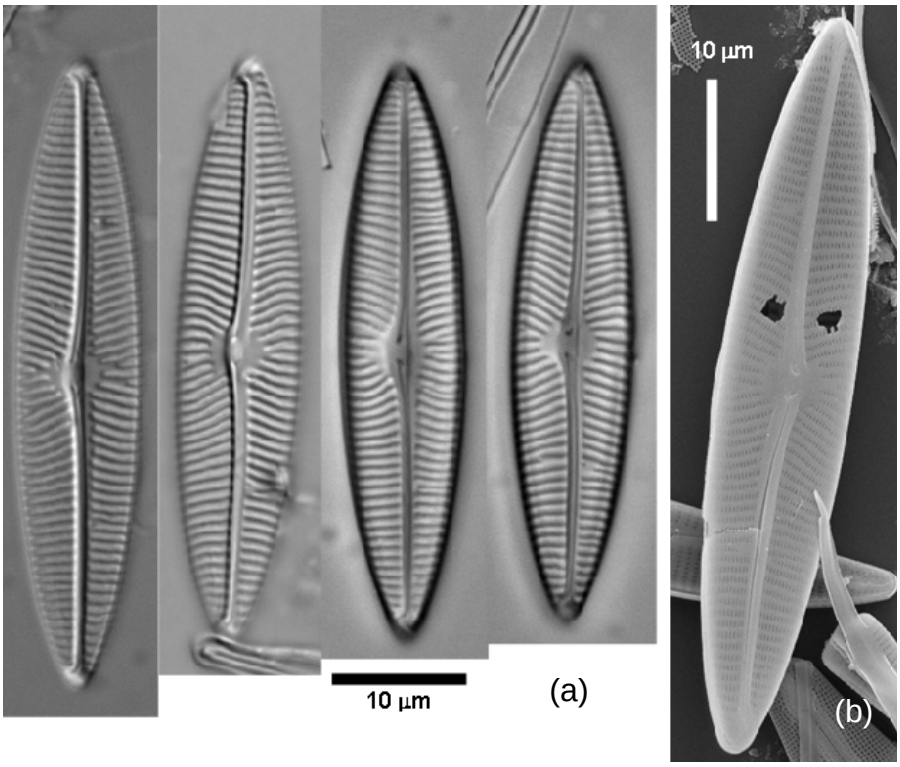


Figure VI.25
Navicula sp. A.
(a) LM, size declination;
(b) SEM, external valve view.

Comments: The general features and fine structure of this species places it within *Navicula* as defined by Cox (1999). In most *Navicula* species, the raphe has a straight path, though it is curved in some, e.g., *N. obtecta* Jüttner & Cox (Jüttner et al. 2000) and *N. kohlenbachii* Lange-Bertalot & Rumrich (Rumrich et al. 2000), as it is in the present species. At this stage I have located no species that matches the Bealey species in outline, dimensions, striae arrangement, etc. However, because of the very large number of *Navicula* species, and a lack of distinctive features in the Bealey population, I have assigned this species to the "Undetermined" range category (Table VI.1).

Genus *Neidium*

The freshwater diatom genus *Neidium* contains over 300 taxa (Hamilton and Jahn 2005), most of which are typically encountered in acidic, low-alkalinity waters. The genus is very distinctive (Round et al. 1990), but many named species appear morphologically similar to each other while

others show great intra-specific variation (Patrick and Reimer 1966). One *Neidium* taxon was commonly observed in the material from Bealey.

***Neidium iridis* (Ehrenberg) Cleve (Figure VI.26)**

Description of specimens from Bealey: Valves elongated and elliptical, with convex sides tapering to rounded apices. Length: 89 – 100 μm, breadth 21 – 22 μm, striae 18 in 10 μm. Narrow axial area, with a further slight narrowing at the apices and towards the central area. Central area transversely elliptical, sometimes slightly diagonal. Central raphe endings tightly curved in opposite directions, distal raphe end appears forked due to a V-shaped silica flap covering the end. Striae punctate (16 – 18 puncta per 10 μm), slightly radiate or oblique at the centre of the valve,

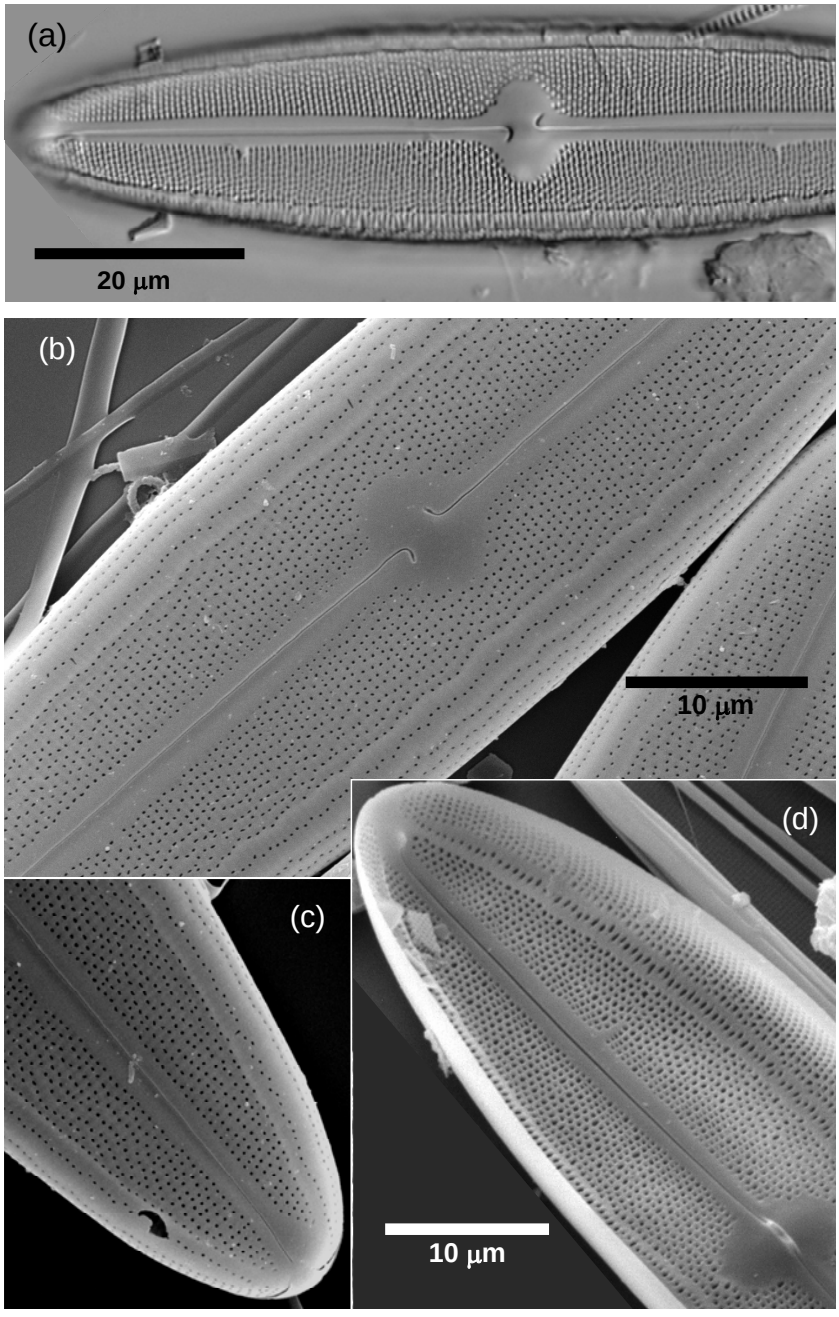


Figure VI.26

Neidium iridis.

(a) LM, valve view;

(b) SEM, external valve view, centre;

(c) SEM, external view showing raphe end;

becoming parallel and then slightly divergent towards the apices. Longitudinal bands at the valve edge are characteristic for *Neidium* and in the Bealey populations comprise a longitudinal row of areolae set apart from the striae, then 3 or more closely-spaced additional rows separated from the first one by a wider space, continuing over onto the mantle as striae. In many specimens, the bands are very slightly constricted at the centre of the valve.

Comments: The Bealey specimens correspond precisely to descriptions and illustrations of *N. iridis* in Patrick and Reimer (1966) [p. 387, Pl. 34., fig. 1] and Krammer and Lange-Bertalot (1997) [Vol 2/1, p. 279, Fig. 104, Fig.1]. The latter authors describe the species as much more variable than the former, and not all their illustrations are consistent with specimens from Bealey. However our populations certainly do not differ in any respect from some forms of *N. iridis* from both Europe and North America. Therefore it is concluded that the Bealey populations represent a cosmopolitan species.

N. iridis was found predominantly in pools with pH < 6.2.

Genus *Pinnularia* Ehrenberg

Pinnularia is a diverse genus that may comprise over 1500 species worldwide (Krammer 2000). The genus is easily recognizable, but the huge number of named species in existence, and intra-species variability, leads to difficulty both in assigning specimens and populations to named species and in describing new species. Indeed, the introductory pages in Krammer (2000) are devoted to a discussion of the species concept in diatoms, including a plea for strict requirements for describing new species, yet acceptance that there is at least some evidence for the existence of many cryptic diatom species.

At least four species of *Pinnularia* were distinguished from the samples at Bealey, and the three most common are described below.

***Pinnularia macilenta* Ehrenberg (Figure VI.27)**

Description of Bealey material: Valves elongated and nearly linear, with slightly convex sides. Large specimens are slightly swollen in the middle and at the ends (i.e., slightly capitate). Length: 67 – 98 μm, breadth 11.9 – 13.2 μm, 8.5 to 10 striae in 10 μm, with slightly increased density towards the apices. Striae radiate in the centre, convergent at the ends, with an irregular fascia (gaps in the striae adjacent to the central area). Raphe slightly off-centre in an axial area covering up to a third of the valve width, narrowing towards the apices and widening to a central area spanning up to three-quarters of the valve width. Central raphe endings curved to one side, and

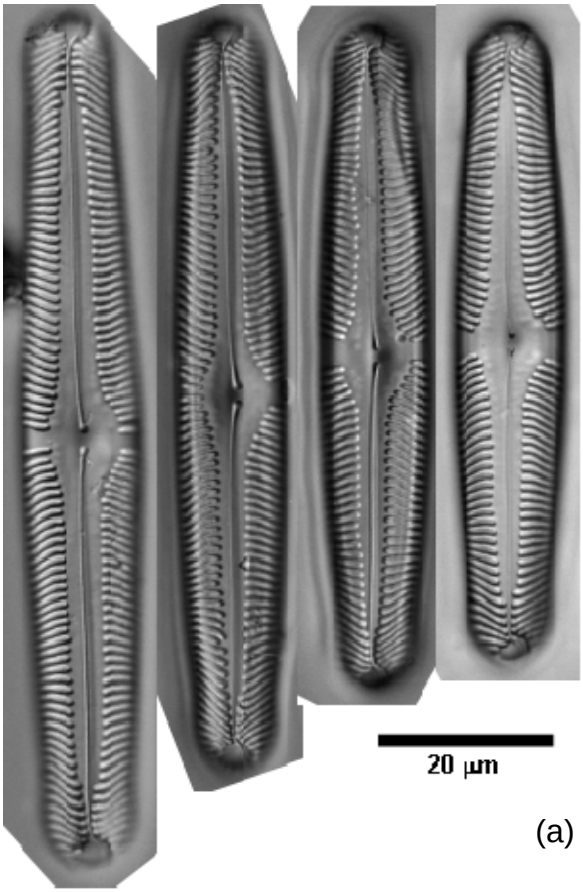


Figure VI.27

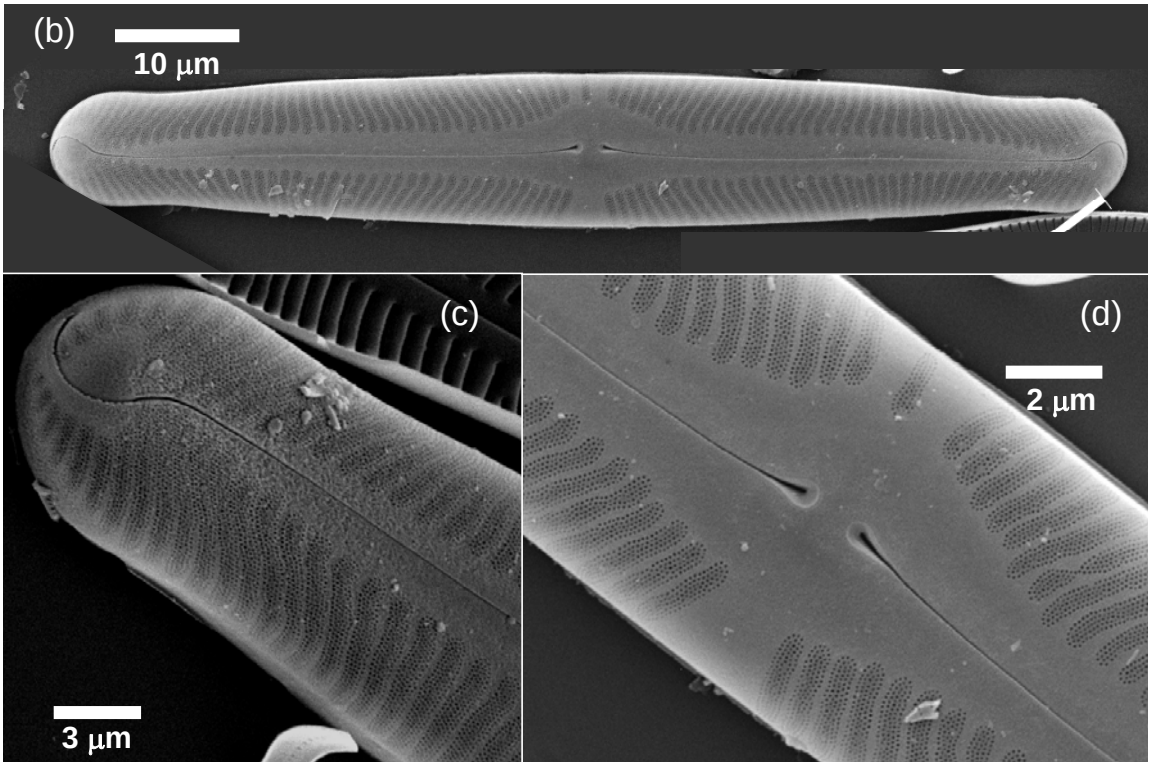
Pinnularia macilenta.

(a) LM, size declination;

(b) SEM, external view;

(c) detail of terminal fissure;

(d) detail of central pores.



with rounded central pores. Distal raphe endings question-mark-shaped. In most specimens, indistinct markings are visible in the central area, more or less as described for *P. macilenta* (Krammer 2000).

Comments: This species was placed in *Pinnularia subgibba* Krammer in Kilroy et al. (2006 [II]), based on the description and illustrations in Krammer (1992). In his more recent treatment of *Pinnularia*, Krammer (2000) transferred *P. subgibba* var. *hustedtii* to *P. macilenta*, and also illustrated the latter species with populations from New Zealand, Guyana and Europe.[3] The populations at Bealey conform to the description of *P. macilenta* except that the valves tend to be broader [length to breadth ratio 6 to 7.4, rather than 6 – 10 stated in Krammer (2000)], and the striae cover a slightly larger proportion of the valve width. In the latter respect, the Bealey populations are closer to *P. subgibba* but have a markedly lower length to breadth ratio (7 – 8 in *P. subgibba*). Krammer (2000) separated *P. macilenta* from *P. subgibba* only by their "size range of whole life cycles". The populations from Bealey show such close affinities to *P. macilenta* in particular that it is difficult to justify separating them into different species. Also note that both the Bealey populations and those illustrated in Krammer (2000) show quite variable stria length and axial area widths, and individual specimens from the different locations match each other very closely.

Pinnularia macilenta occurred sporadically only in pools with pH < 6.2

***Pinnularia* sp. A (Figure VI.28)**

Description of Bealey material: Valves linear - elliptical with convex sides tapering smoothly to bluntly rounded ends (cigar-shaped). Length: 64 – 94 μm, breadth 13.1 – 15.5 μm, 7 to 9.5 striae in 10 μm, with slightly increased density towards the apices. Striae radiate in the centre, convergent at the ends, usually with an irregular fascia at the centre, on one or both sides. Axial area gradually widening from the ends to the centre to a central area spanning about two-thirds to three-quarters of the valve width. Raphe slit more or less central with a very slight undulation discernible in many specimens (and in SEM). Central raphe endings bent to one side, and with rounded to drop-shaped central pores. Distal raphe endings question-mark-shaped, very clear in LM. Indistinct markings are visible in the central area, as in *P. macilenta* (see above).

Comments: *Pinnularia* sp. A was initially thought to be close to *P. oriunda* Krammer (Kilroy et al. 2006 [II]). However, the latter taxon possesses a longitudinal band[4], which is not present in sp. A. These populations of *Pinnularia* presented an identification problem because of their similarity to *P. macilenta*, especially smaller specimens. The two species differed in outline (no suggestion of capitate endings in sp. A), width (largely non-overlapping width range), and slightly coarser stria

[3] Krammer (2000) pointed out that earlier authors had misinterpreted *P. macilenta*. For example, the illustration in Schmidt's Altlas (Schmidt et al 1874 - 1959) shows a very different taxon from that in Ehrenberg's original material (see Plate 63, fig. 5 in Krammer 2000).

[4] Many species of *Pinnularia* are characterised by possession of longitudinal bands visible in LM as a discontinuity in the striae. The effect is a result of closure of the internal areolae slits with a plate of silica.

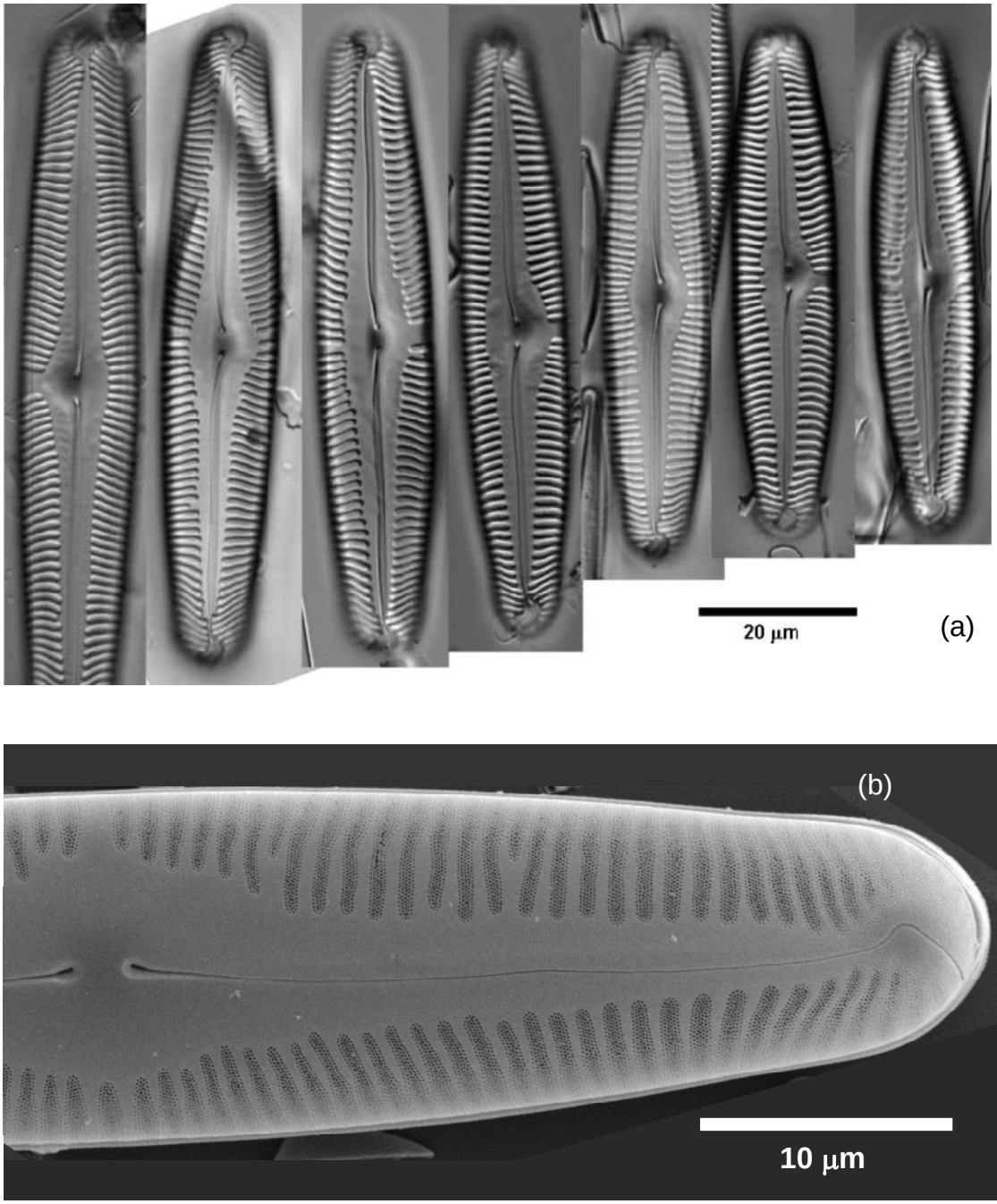


Figure VI.28 *Pinnularia* sp. A. (a) LM, size declination; (b) SEM, external valve view.

density in sp. A (on average). Their fine structure was similar (under SEM), except that the terminal raphe fissures differed in shape. In *P. macilenta* the fissure formed a smooth curve over the rounded end of the valve; in *Pinnularia* sp. A, they curved more sharply farther back on the valve face (compare Figures VI.27c and VI.28b). Although the species were recorded co-existing in the same pools *P. macilenta* was much more common in the more acidic pools (but not in all of them) while *Pinnularia* sp. A occurred in highest densities in the less acidic pools.

***Pinnularia biceps* Gregory (Figure VI.29)**

Description of Bealey material: Valves elongated, linear with almost straight to triundulate margins, with definitely capitate ends, narrower than the rest of the valve. Length: 60.5 – 77 μm, breadth 12.3 – 13.7 μm, 9.5 to 11 striae in 10 μm. Striae radiate in the centre, convergent at the ends, with an irregular fascia in some specimens. Straight raphe in a narrow axial area widening to a rhombic central area. Central raphe endings curved to one side, and with noticeable central pores. Distal raphe endings question-mark-shaped.

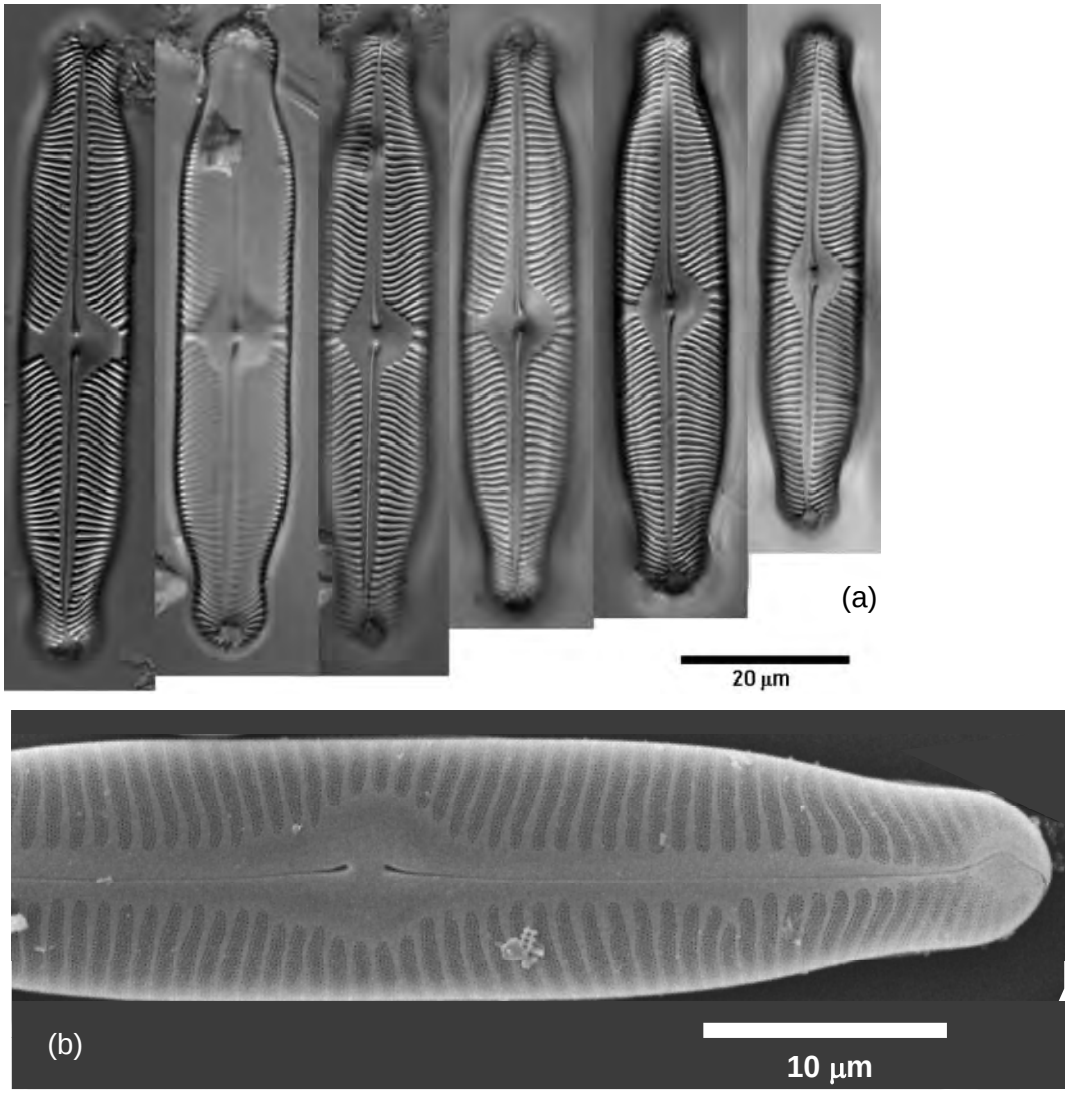


Figure VI.29 *Pinnularia biceps*. (a) LM, size declination; (b) SEM, external valve view.

Comments: Shape, dimensions, striae arrangement, variability of the fascia within populations, and length to breadth ratios in the Bealey material correspond exactly with those described and illustrated for *P. biceps* in Krammer (2000). Krammer (2000) shows specimens from Finland, Scotland and "Middle Europe", indicating a cosmopolitan taxon.

Genus *Stenopterobia* Brebisson ex Van Heurck

Stenopterobia was first described in 1899 with species transferred from the closely related genus *Surirella* Turpin. *Stenopterobia* is distinguished from *Surirella* by its narrow, elongated and sometimes sigmoid (S-shaped) outline, and isopolarity along the apical axis (as opposed to frequent heteropolarity in *Surirella*). The genus is confined to acidic, oligotrophic waters, including ombrogenic mires (Round et al. 1990), whereas *Surirella* is found across a very broad range of aquatic habitats. This small genus currently has less than about 15 species (see Lange-Bertalot and Metzeltin 1996, Krammer and Lange-Bertalot 1997, Rumrich et al. 2000, Brassac et al. 2003, Siver and Hamilton 2005). Three species were identified from the Bealey material.

Stenopterobia delicatissima (Lewis) Van Heurck (Figure VI.30)

Description of Bealey material: Valves isopolar, elongated, linear-lanceolate, parallel in the central part of the valve and tapering to very narrow apices. Length: 67 – 77 μm, breadth 4.2 – 4.6 μm, 65 – 72 fibulae per 100 μm (apertures through the valve centre, raising the raphe canal on a series of struts). Striae 25 – 27 per 10 μm, separated by small raised costae (ribs), with each stria comprising 2 – 3 rows of tiny areolae. The striae are broken at the centre by a lanceolate hyaline area running most of the length of the valve.

Comments: Krammer and Lange-Bertalot (1997) quote a wide range of stria and fibula density for this taxon (Table VI.1) and illustrate quite variable populations from different locations. The Bealey populations are indistinguishable in dimensions, shape, and fine structure from specimens from northern Europe (Krammer and Lange-Bertalot 1997, Plates 173-174) and South America (Metzeltin and Lange-Bertalot 1998, Plate 218; Rumrich et al. 2000, Plate 197), and are therefore assumed to belong to this cosmopolitan taxon.

Stenopterobia cf. *curvula* (W. Smith) Krammer (Figure VI.31)

Description of specimens from Bealey: Valves isopolar, elongated, narrow, linear with a slightly sigmoid outline. All specimens observed had slightly capitate endings, swollen to a somewhat rhombic shape. Length: 145 – 180 μm, breadth 6.1 – 7.1 μm, 35 – 40 fibulae per 100 μm. Striae 21 – 22 per 10 μm, separated by small raised costae, with each stria comprising 2 – 3 rows of tiny areolae. The striae are broken at the centre by a very narrow hyaline area (a depression externally) running the entire length of the valve. The ribs bear raised, flattened spinules (like mushrooms) of varying size (Figure VI.31b,d).

Comments: Illustrations of *St. curvula* generally show specimens with valves tapering to narrow, rounded apices (e.g., Krammer 1987, Lange-Bertalot and Metzeltin 1996, Krammer and Lange-Bertalot 1997, Beier and Lange-Bertalot 2007). However, the Krammer and Lange-Bertalot (1997)

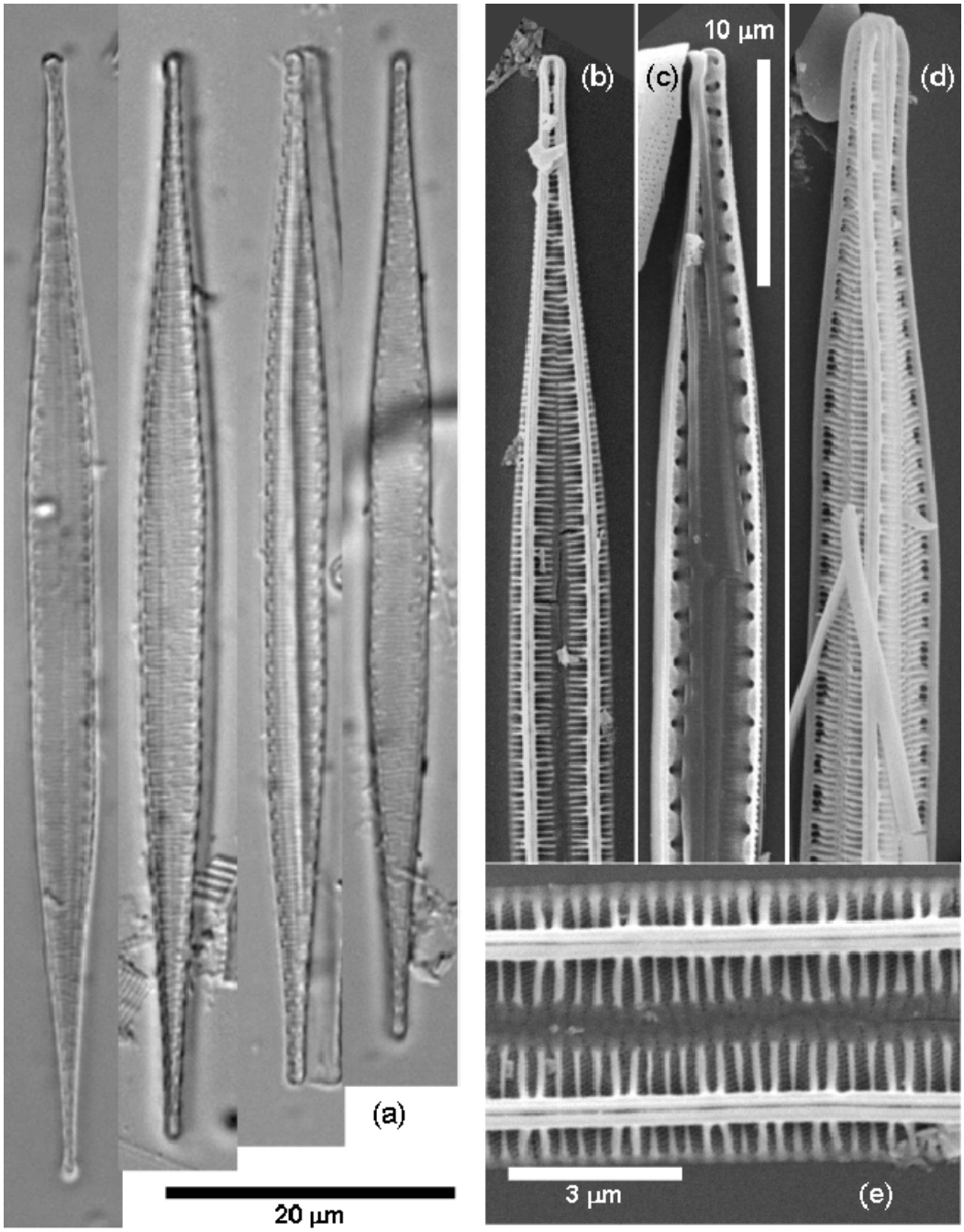


Figure VI.30 *Stenopterobia delicatissima*. (a) LM, size declination. (b), (d), (e) SEM, external views; (c) SEM, internal view.

description of the valve ends also includes "…etwas kopfförmig erweitert und dann rhombisch abgerundet …". This form is illustrated in Lange-Bertalot and Metzeltin (1996) from a Finnish lake, and the Bealey taxon was assigned to *St. curvula* in II on the basis of its correspondence to the Finnish taxon. The fine structure of the Bealey specimens shows strong similarities to that in *St. delicatissima*, viz. pairs of ribs join directly to (and support) the raphe canal, separated by 2 to 5 ribs that connect below the raphe canal (see Figures VI.30e and VI.31b). This concurs with the first

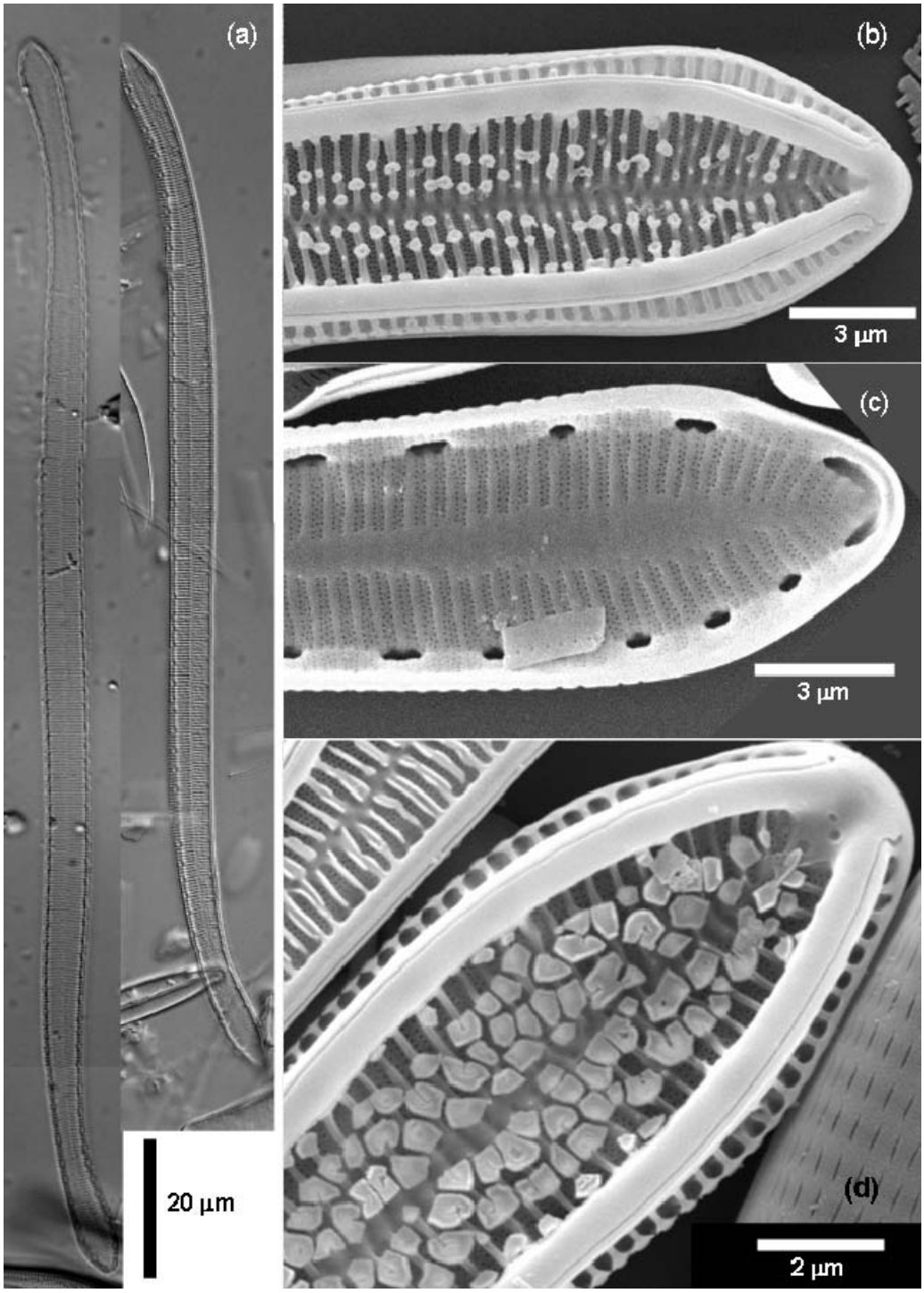


Figure VI.31 *Stenopterobia* cf. *curvula*. (a) LM, size range. (b), (d) SEM, external views (detail); (c) SEM, internal view.

detailed description of the two species (Krammer 1989), who stated: "The valve structure of *Stenopterobia delicatissima* … is identical with that of *St. curvula*…". I have found it difficult to reconcile this with SEM illustrations in Krammer and Lange-Bertalot (1997, Plate 170), which suggest similar structure in *St. delicatissima* and *St. densestriata*, but a contrasting structure in *St. curvula*. Whether this form of the species represents a different taxon from *St. curvula* remains to

be investigated, hence I assign it to *St.* cf. *curvula*. Nevertheless, on the basis of correspondence with a Northern Hemisphere taxon (above) I conclude that this species is cosmopolitan.

Stenopterobia sp. A (Figure VI.32)

Description of specimens from Bealey: Valves isopolar, elongated, narrow, linear with a slightly sigmoid outline. Ends tapering gradually to narrow rounded apices. Length: 85 – 140 µm, breadth 4.5 – 5.5 µm, 50 – 55 fibulae per 100 µm. Striae 26 – 27 per 10 µm, separated by small raised costae, with each stria comprising 2 – (usually) 3 rows of tiny areolae. Each costa appears to be

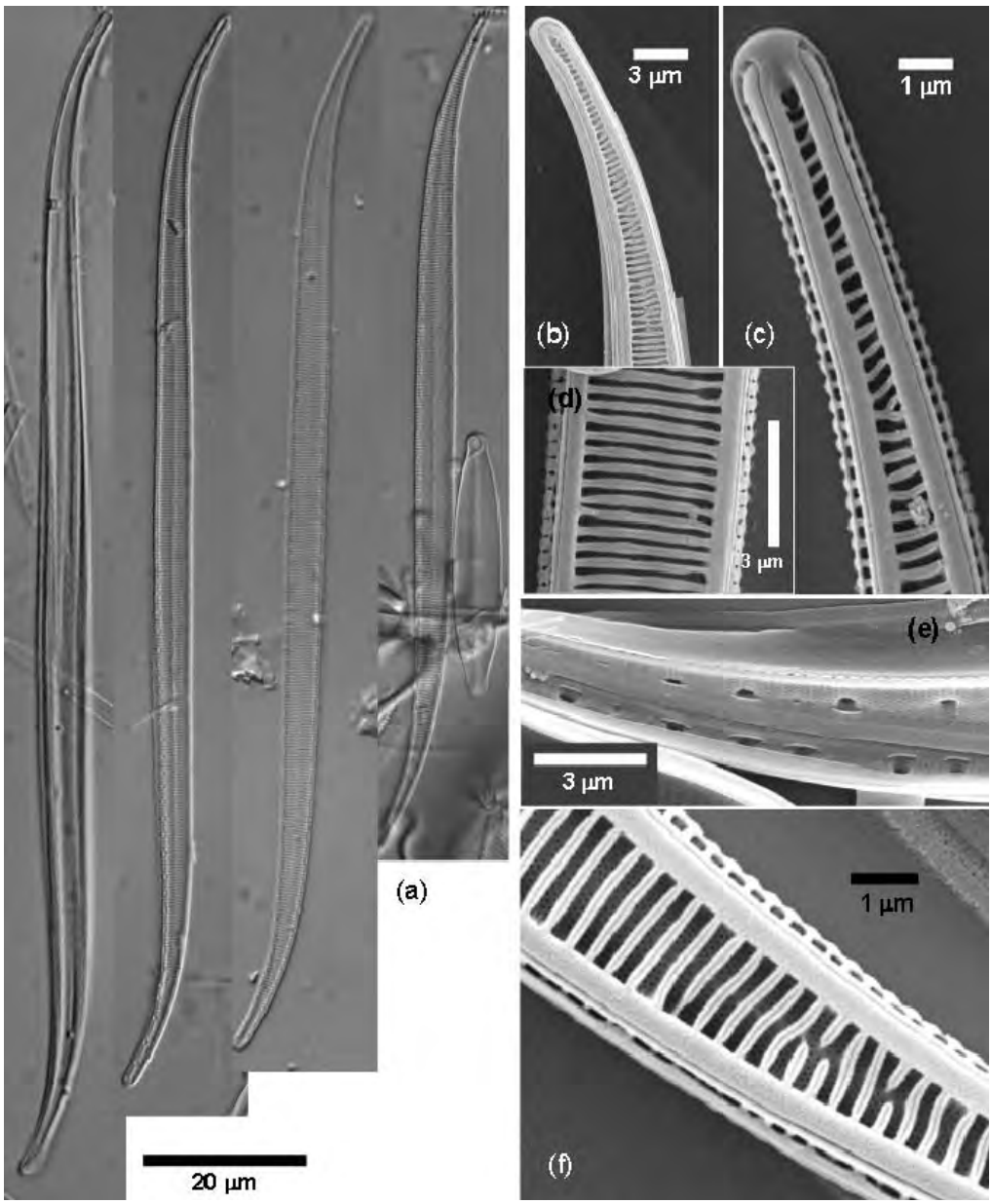


Figure VI.32 *Stenopterobia* sp. A. (a) LM, size declination. (b) – (d), (f) SEM, external views; (e) SEM, internal detail.

double though this may be at the surface only (Figure VI.32f). There is a central break in the striae but the costae often span the entire valve width (Figure VI.32d). Almost all costa appear to be joined directly to the raphe canal.

Comments: This taxon was initially compared with *St. densistriata* (Hustedt) Krammer (Kilroy et al. 2006 [II]). However, almost all specimens were considerably longer than the range stated for *St. densestriata* and had more strongly curved and narrower, more protracted apices. Indeed in length and outline this taxon is closer to the generally accepted shape for *St. curvula* (see above), though this Bealey species is always narrower and has higher stria density (Table VI.1). I could locate no other known *Stenopterobia* species that resembles our specimens more closely. Its fine structure also appears to set it apart from other known species. The apparent direct connection of all the exterior raised costae to the raphe canal (from both sides – see Figure VI.32d) is similar to the structure described for *St. curvula* by Krammer and Lange-Bertalot (1997), but a lack of a consistent central break or depression in the costae is different. On this basis I conclude that *Stenopterobia* sp. A at Bealey may represent an undescribed and possibly endemic taxon.

Tabellaria Ehrenberg

Tabellaria is easily recognized from its colonial habit (zig-zag colonies) and distinctive cell structure. Only five species are listed in Krammer and Lange-Bertalot (1991) and I can locate only one more recently described variety (*T. flocculosa* var. *andina* Lange-Bertalot; see Rumrich et al. 2000). However, a number of studies have concluded that considerable hidden diversity exists in this genus (e.g., Koppen 1975, Lange-Bertalot 1988, Krammer and Lange-Bertalot 1991, Mou and Stoermer 1992). Unfortunately the diversity is very difficult to recognize without detailed morphometric analysis.

Tabellaria flocculosa (Roth) Kützing (Figures VI.33)

Description of specimens from Bealey: There appear to be several distinct populations of *Tabellaria* at Bealey, which can be distinguished by their outline and stria density (e.g., Figure VI.33a –c). As far as I can ascertain, all have a rimoportula located laterally in the central swollen part of the valve (e.g., Figure VI.33d,e)

Comments: The populations at Bealey conform to the broad description of *Tabellaria flocculosa* in Krammer and Lange-Bertalot (1991), in dimensions and location of the rimoportula, and in formation of zig-zag colonies. Because of the ill-defined nature of this taxon, it is difficult to draw conclusions with regard to their cosmopolitan vs. endemic status. Therefore I *provisionally* assume that these populations represent cosmopolitan taxa, but note that they require further study.

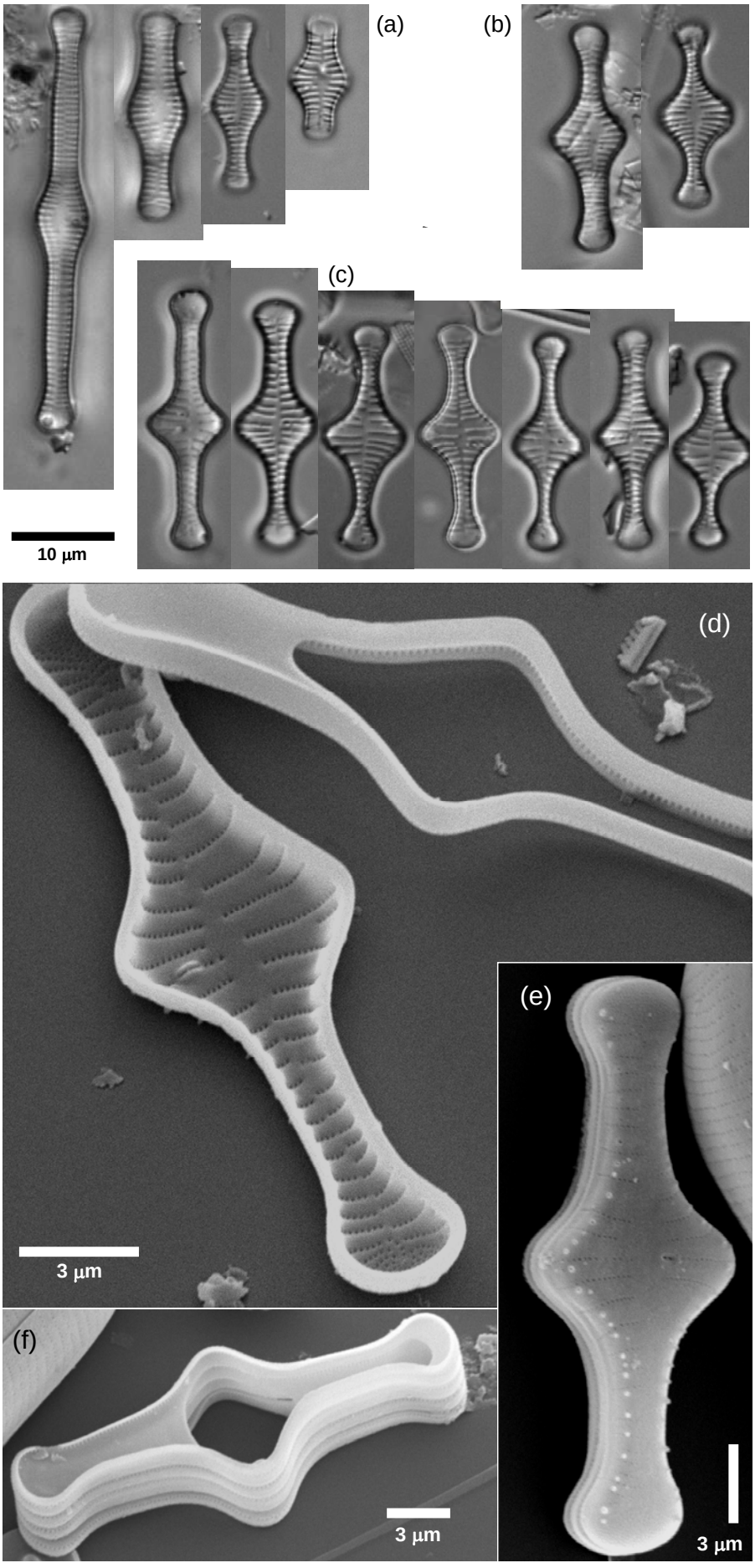


Figure VI.33

Tabellaria flocculosa

(a – c) LM, size declination in three apparently distinctive populations;

(d) SEM, internal valve view, with a girdle band – note the internal processes of the rimoportula;

(e) SEM, external valve view – note small spines;

(f) SEM, a stack of girdle bands.

Discussion

As H. Lange-Bertalot pointed out in Krammer (2000) [and as many taxonomists have pointed out in the past], any species identification and particularly any description of a new species is an hypothesis, which can be supported or refuted. The above species assignments to existing or new taxa and conclusions with regard to geographical distribution are accordingly hypotheses only, based on a synthesis of information available at the time of writing. As discussed in the descriptions, many assignments proved difficult, and sometimes indeterminate. This was unavoidable simply because there are so many known diatom species, many of which have been described only recently. To minimize the chances of overlooking a matching taxon the widest possible range of literature was consulted, and careful comparisons were made of specimens from Bealey populations with all similar species in the literature. A further difficulty was that morphological differences between known species and those found in the Bealey samples could be quite subtle. Because subtle morphological differences between populations have been shown to represent both phenotypic plasticity in response to ecological variability (Cox 1994) and reproductively isolated co-existing populations (Droop et al. 2001, Mann et al. 2004), justification for erecting new species must be rigorous.

In the above analysis, I attempted to adopt consistent "rules" to guide decision-making. First, if two populations differed only in size range, with the size ranges overlapping, then I concluded that the Bealey population *most probably* belonged to the existing taxon, even if its size limit was beyond the maximum and/or minimum of the existing taxon.

Second, a new taxon was proposed if the Bealey populations showed at least two of the following with respect to the closest existing species (from the literature):

1. largely non-overlapping size range;
2. a clearly and consistently different outline (shape);
3. clearly and consistently different internal dimensions / structures visible in LM, e.g., stria density, raphe arrangement, central area;
4. clearly and consistently different internal structures visible in SEM, e.g., areola structure, raphe endings.

Inclusion of the word "clearly" in 2, 3 and 4 above introduces a degree of subjectivity into the decision-making. This is inevitable because the literature already includes descriptions of species within which variability of shape and dimensions are accepted (e.g., *Brachysira brebissonii*, in Lange-Bertalot and Moser 1994). There are also examples in the literature of species assignments in diatoms on the basis of apparently small differences which have been shown to represent reproductively isolated species (e.g., *Sellaphora* complex, Mann et al. 2004). As Kociolek (1998) remarked with respect to defining genera, the evolutionary history of the taxon also needs to be taken into account. Thus, a *combination* of characters will define the relationship between taxa. Without detailed genetic or reproductive studies, the decision to assign species status to two

different populations that share some features but not others must always, ultimately, be subjective (i.e., an hypothesis).

An additional consideration is that size declination in diatoms as part of the cell cycle means that each species has an intrinsic range of both size and shape. (See Round et al. 1990, pp. 82 – 84 for a general discussion of cell size reduction in diatoms.) In the present account, the natural size range of a species has been accounted for by examining populations of a species rather than individual specimens, as is recommended practice in describing and defining diatom species (e.g., Mann 1999).

All species assigned new taxon status were assumed to be *most probably* endemic to New Zealand. The range within New Zealand could not be defined, although in some cases, the taxon had been observed in other locations in New Zealand (e.g., *Frustulia* sp. A, *Brachysira* sp. A, see Kilroy et al. 2007 [I]). As Finlay et al. (2002) pointed out, it is impossible to prove that a species does *not* exist in other locations, especially if that species is rare. Many of the species assessed in this account as most probably endemic were certainly not rare locally (see Table VI.1). For these more common taxa we may have more confidence that if they were distributed worldwide then they would have been previously reported from other locations.

All nine taxa found to be indistinguishable from cosmopolitan taxa have been reported from multiple locations worldwide, which is consistent with the idea of a core of common cosmopolitan taxa (Kociolek and Spaulding 2000). These are presumably weedy, adaptable, easily transportable species that are constantly being redistributed through human and other means of transport. The corollary to this idea is that many more species have restricted distributions because they are less transportable. Nevertheless, these must have evolved from more widely distributed taxa. Thus, the Southern Hemisphere in general, and the New Zealand – Tasmania – Eastern Australia region in particular – have flora containing species clearly related to, but different from those in the Northern Hemisphere. There is an analogy to this in higher plants in that, according to McGlone et al. (2001), most vascular plants arrived in New Zealand, via long-distance dispersal, during the late Miocene or early Pleistocene. The subsequent changing climate and landscape lead to adaptation and specialization of the flora to the new conditions, i.e., the evolution of endemic species. If the diatom flora followed a similar pattern, we would expect to find endemic species that have affinities with their parent taxa, but with specializations that confine them to their current environments. *Eunophora* appears to be one of only a few diatom genera that are largely confined to the Southern Hemisphere. Another example is *Actinella*, most species of which have a tropical or Southern Hemisphere distribution (Sabbe et al. 2001).

2.VII New species of *Fragilariforma* (Bacillariophyceae) from New Zealand and Australia

Introduction

The genus *Fragilariforma* Williams and Round was erected to include "several species that have been closely associated with *Fragilaria sensu stricto* because of their colony formation, but [the genus] is distinguished by the slight or absent sternum" (Williams and Round 1987). The genus was initially described as *Neofragilaria* (Williams and Round 1987) but species were subsequently transferred to the new genus *Fragilariforma* as the name *Neofragilaria* had been pre-empted (Williams and Round 1988). Species in *Fragilariforma* possess small discoid plastids and form linear or zig-zag colonies. Ultrastructural features include open girdle bands, each bearing a row of poroids, simple apical pore fields, and a single polar rimoportula aligned with a stria (see also Round et al. 1990). Six species were transferred from *Fragilaria* to *Fragilariforma* by Williams and Round (1987, 1988). Several others were named as very likely belonging to *Fragilariforma*; some of these and others have since been transferred to the genus (Table VII.1).

Only one representative of the genus *Fragilariforma* (*Fragilariforma virescens* (Ralfs) Williams and Round) has been reported in New Zealand (Cassie 1984, V. Cassie Cooper pers. comm.) to date, apart from a tentative identification of *F. constricta* f. *stricta* (A. Cleve) Poulin (Cassie 1989).

In recent collections of diatoms from sub-alpine oligotrophic and dystrophic waterbodies on Stewart Island and South Island, New Zealand, we encountered cruciform to rhombic araphid diatoms that did not correspond well with commonly known species with these shapes (for example, as listed in Krammer and Lange-Bertalot 1991). Some of the Stewart Island samples also contained narrow, elongated forms with a constriction at the centre of the valve. The cruciform/rhombic diatoms from Stewart Island have formerly been identified as *Fragilaria construens* (Ehrenberg) Grunow (V. Cassie Cooper pers. comm.). Vyverman et al. (1995) identified similar diatoms collected from lakes in Tasmania as *Fragilaria construens* (Ehrenberg) Grunow, *Fragilaria lata* (Cleve-Euler) Renberg, and forms of *Fragilaria constricta* Ehrenberg, on the basis of size, shape, and stria counts, but with the qualifier that further investigations were needed to establish their taxonomy. Examination under light (LM) and scanning electron microscopy (SEM) has revealed features that place these diatoms in the genus *Fragilariforma*, as it is currently defined, and separate them into at least two distinct species. In this paper we discuss the New Zealand collections in detail, with reference to the Tasmanian material and to further material found in a sample from mainland Australia during the course of this investigation. Two new species, *Fragilariforma cassieae* and *Fragilariforma rakiuriensis*, are described and the possible existence of further species is suggested. We discuss their relationships to existing species

Table VII.1 Species currently placed in *Fragilariforma*, and related taxa mentioned in Williams & Round (1987)[a]

Species	Shape	Areolae	Rimoportulae	Type location	Ecology[b]	References
Fragilariforma virescens (Ralfs) Williams & Round	Elongated linear to elliptical	Small poroids	One	Cosmopolitan[c]	Oligotrophic, circumneutral, pH 6.48	Krammer & Lange-Bertalot 1991, Camburn & Charles 2000
Fragilariforma cassieae sp. nov.	Rhombic with narrow, protracted apices	Small poroids in round depressions, 28-30/10μm	None	New Zealand, Tasmania, mainland Australia	Low conductivity, circumneutral	This study
Fragilariforma rakiuriensis sp. nov.	Narrow, bi-undulate to rhombic with narrow, protracted apices	Small poroids, externally occluded	None	New Zealand, Tasmania, mainland Australia	Acid? (not determined yet)	This study
Fragilariforma acidobiontica (Charles) Williams & Round	Elongated linear to linear-lanceolate	Small poroids, ~50/10 μm	labiate process (both apices?)	North America	Acid waters, pH 4.48, alkalinity 11±1.6 μeq	Charles 1986
Fragilariforma bicapitata (A.Mayer) Williams & Round	Elongated linear to elliptical, capitate	Unknown	At one or both apices	Northern Hemisphere, Chile	Poorly defined	Krammer & Lange-Bertalot 1991
Fragilariforma constricta (Ehrenberg) Williams & Round	Bi-undulate (constricted) to rhomboid	"centrally perforate cribra"	Unknown	Falkland Islands	pH 5.57, alkalinity 18±2.1 μeq	Williams & Round 1987, Krammer & Lange-Bertalot 1991
Fragilariforma constricta f. *stricta* (A.Cleve) Poulin	Wide bi-undulate to broadly elliptical	Unknown	Unknown	Northern Europe?	Slightly acid, pH 5.82, low conductivity	Krammer & Lange-Bertalot 1991, Camburn & Charles 2000
Fragilariforma constricta f. *trinodis* (Hustedt) Hamilton	Tri-undulate	Unknown	Unknown	Northern Europe	Acid?	Simonsen 1987, Kingston et al. 2001
Fragilariforma constricta f. *tetranodis* (Hustedt) Hamilton	Bi-undulate with secondary undulations	Unknown	Unknown	Northern Europe	Acid?	Kingston et al. 2001
Fragilariforma costatum (Rehakova) Williams	Elongated (?)	Unknown	?	"Czechoslovakia"	[Fossil]	Williams 1996a
Fragilariforma floridana (Hanna) D.M. Williams	Cruciform	Poroids	Unknown	North America	No details	Williams 1990

Fragilariforma hungarica (Pantocsek) Hamilton	Rhomboid	Unknown	Unknown	Northern Europe?	Unknown	Pantocsek 1902, Cleve-Euler 1953
Fragilariforma hungarica var. *tumida* (Cleve-Euler) Hamilton	Rhombic with blunt, protracted apices	Unknown	Unknown	Northern Europe ?	pH 5.59	Cleve-Euler 1953, Camburn & Charles 2000, Kingston et al. 2001
Fragilariforma lata (A. Cleve-Euler) Williams & Round	Bi-undulate (constricted) to rhombic with narrow, protracted apices	Small poroids, 50/10 μm	None	Northern Europe	Oligotrophic, circumneutral to acid, pH 5.61, alk. 18±2 μeq	Renberg 1977, Camburn & Charles 2000 (SEM)
Fragilariforma platensis Williams	Linear – elliptical	Small poroids	Rare	Argentina	[Fossil]	Williams 1996a
Fragilariforma polygonata (Cleve-Euler) Kingston, Sherwood & Bengsston	Tri-undulate to rhombic with blunt, protracted apices	Unknown	Unknown	Northern Europe?	Alkalinity 8±1.8 μeq	Cleve-Euler 1953, Kingston et al. 2001
Fragilariforma strangulata (Zanon) Williams & Round	Elongated, linear	Poroids in round depressions, ~30/10 μm	Unknown	Central Africa	"aquis dulcibus"	Williams & Round 1987
[a]*Fragilaria braunii* Hustedt	Narrow, lanceolate	Unknown	Unknown	Brazil	No details	Simonsen 1987
[a]*Fragilaria javanica* Hustedt	Linear-lanceolate, capitate	Unknown	Unknown	West Java	No details	Simonsen 1987, Scherer 1988
[a]*Fragilaria nitzschioides* Grunow in Van Heurck	Elongated linear to narrowly elliptical	Small poroids(?), 40–50/10 μm	Unknown	Uncertain	Poorly defined	Krammer & Lange-Bertalot 1991, Patrick & Reimer 1966
[a]*Fragilaria sioli* Hustedt	Elongated, linear, capitate	Unknown, prominent in LM	Uncertain	Brazil	Unknown	Simonsen 1987
[a]*Fragilaria sublineata* Hustedt in A.Schmidt	Linear, elongated	No details	Unknown	East Africa	Unknown	Schmidt 1913
[a]*Fragilaria telum* Carter & Denny	Elongated, linear, capitate	~36/10 μm	Unknown	Sierra Leone	No details	Carter & Denny 1987

[a]Apart from the *Fragilaria* species transferred to *Fragilariforma* in Williams & Round (1987, 1988), several other possible candidates for the genus were mentioned. These are included above, with the exception of *F. denestriata* Hustedt and *F. obtusa* Hustedt, which do not seem to be consistent with *Fragilariforma* according to illustrations in Simonsen (1987).

[b]Alkalinities taken from Fallu et al. (2000); pH values from Camburn & Charles (2000).

[c]Note that *F. virescens* is usually thought of as cosmopolitan, but this assumption should be interpreted with care. For a related example see Williams (1996b).

and with previous interpretations of similar forms. We also consider the defining characteristics of *Fragilariforma* and the status of the two new species within the genus.

This study is linked to ongoing investigations of the freshwater diatom flora of the Australasian region, which are identifying an increasing degree of endemism in the area (e.g., *Gomphoneis minuta* var. *cassieae* in New Zealand, Kociolek and Stoermer (1988); the genera *Biremis* and *Eunophora* in Tasmania and New Zealand, Vyverman et al. (1997, 1998); several *Actinella* species in Australia, New Zealand, and Papua New Guinea, Sabbe et al. (2000, 2001)). The work also forms part of a programme investigating biodiversity in freshwater habitats in New Zealand.

Materials and methods

Samples of epilithon and/or sediment were collected from freshwater habitats in subalpine areas of New Zealand from 1997 to 2002. Organic material in subsamples was digested using concentrated sulphuric acid followed by hydrogen peroxide, and then rinsed up to eight times in distilled water. Drops of the resulting suspension were dried onto cover slips, mounted on slides with Naphrax (Northern Biological Supplies) using the method recommended by the supplier, and examined using a Leica DMLB or a Zeiss Axioplan 2 equipped with differential interference contrast (DIC) optics (LM). Cover slips with the dried material were also mounted on aluminium stubs for examination under a Leica S440 scanning electron microscope or a Jeol JSM-840 operated at 15 kV (SEM). Material from some samples was examined live.

Samples collected from the following locations contained populations of the *Fragilariforma* species under discussion:

Arthur's Pass National Park, Jordan Saddle, pool (part of stream system) (NIWA collection, samples 226, 694, 700);

Stewart Island, Table Hill and Rakeahua Valley, tarns/pools/seeps (NIWA collection, samples T2, 327, 348, 382, 647);

Stewart Island, Little Mt Anglem, small tarn (NIWA collection, sample A5);

Stewart Island, Deceit Peaks, rocky open creek at 500 m (NIWA collection, sample A6);

We also examined slides of samples collected from Tasmania and mainland Australia between 1994 and 1995 and found populations of the taxa of interest from the following locations: Tasmania, Clarence Lagoon, Picone lake and Sappho lake (GENT collection, diverse samples); Mount Kosciusko, Australia, tarn/river (GENT collection, sample 940122).

Measurements of valve length and width (widest point), stria density, and areola density (in LM where possible) were made on as many specimens as possible for each population examined (generally at least 15 specimens of *F. cassieae* and 10 for *F. rakiuriensis*). Terminology and measurement procedures follow Anon. (1975) and Ross et al. (1979). We compared our material with similar taxa using type specimens or type material where possible. We also checked

descriptions and illustrations for a range of possibly related species that are now placed in *Fragilariforma* (Table VII.1).

The following archived material was examined: a) Slides from Cleve-Euler's collection, Swedish Museum of Natural History, Dept. of Botany, Stockholm, from the localities named in the original descriptions of *Synedra parasitica* (Wm. Smith) Hustedt var *genuina* f. *lata* Cleve-Euler (slides MIC2294 – MIC2298 (Lycksele Lappmark, Örträsk, Sweden, leg. Åke Berg), S122585 – S122588 (Örträsk (site 1) Umeå, Sweden)); *Fragilaria hungarica* Pantoscek var. *tumida* Cleve-Euler (slides MIC2315 (Olasjön, Småland, Vislanda parish, Sweden), MIC2301-2302 and S122589-S122590 (Västmanland, Ölsjön, Lindesberg, Sweden), MIC1562-1564 (Kemi Lappmark, Kemijärvi, Finland), MIC1668-1669 (S. Savolaks, Punkaharju, Hekla-ashes, Finland)); b) Slide no. 448, Healey Collection (NIWA, Wellington, New Zealand), containing *Fragilaria undata* Wm Smith (synonym: *Fragilaria constricta* Ehrenberg) (one of Wm Smith's original slide mounts); c) Sample 3206, Lincoln Herbarium; V. Cassie-Cooper, thermal algae collection., ?*Fragilaria constricta*, White Island, Bay of Plenty; d) Ehrenberg collection: sheet 2046 with *Fragilaria constricta* (from the Falklands Is).

Taxonomy

Fragilariforma cassieae C. Kilroy and E.A. Bergey, sp. nov. Fig. VII.1–3

Valvae cum signis principalibus ita ut communiter in genere *Fragilariforma*. Ab omnibus descriptis speciebus generis differt striis distincte punctatis, structura polorum sine spinis instructorum, areis porellorum distinctis. Rimoportulae nullae.

Valves (7)11–27 μm long, 6.2–9 μm wide, rectangular in girdle view. Cells forming zig-zag colonies. Several small discoid plastids. 3 – 5 open girdle bands, each with a row of poroids on the edge facing the epitheca (normally obscured by overlapping of adjacent copulae). In valve view cells rhombic with narrow protracted apices, tending to rhombic with slightly concave sides, to rhombic in very small specimens. Striae 15–18 in 10 μm, distinctly punctate and continuous across the valve and over onto the valve mantle, often with a narrow break along the axial area, sometimes at the centre only. Striae radiate at the centre becoming parallel towards the apices. 26–29 areolae in 10 μm, each a round depression with a centrally placed circular opening through a simple velum. Rimoportula lacking. Marginal spines lie on the interstriae, and are tapering hollow tubes, deflected outwards but may curve back in toward the valve at their tips. Spines absent at the apices. A pore field at each apex comprises about 40 poroids arranged in longitudinal rows extending onto the valve surface. Mantle plaques are often present along the mantle margin.

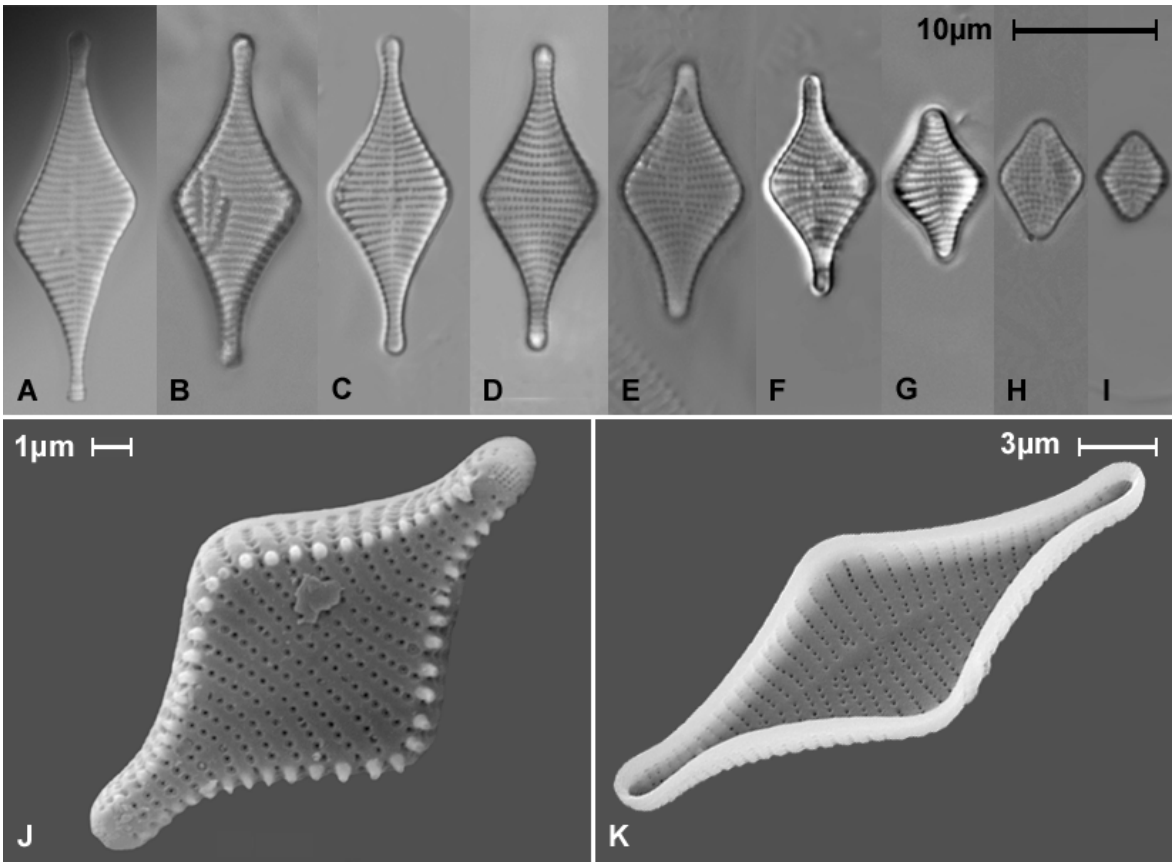


Figure VII.1 *Fragilariforma cassieae*, from the type population, Jordan Saddle, Arthur's Pass, South Island, New Zealand. A-I, morphological progression during cell size reduction (LM); J, SEM of valve face; K, SEM of valve interior.

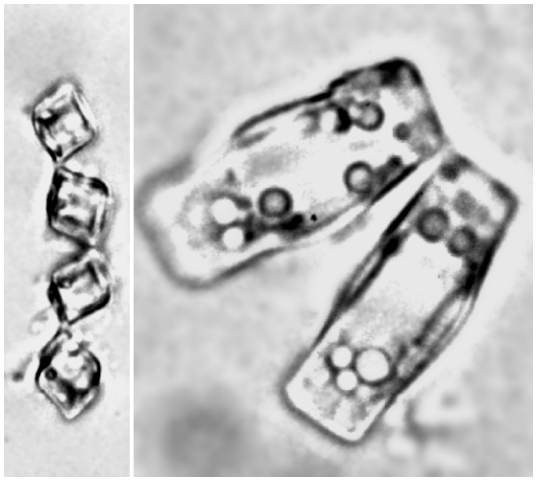


Figure VII.2

Live cells of *Fragilariforma cassieae* from the Jordan Saddle population showing typical formation of pairs of cells joined at their apices (A), or short zig-zag chains (B). Cells are approx. 15 µm long.

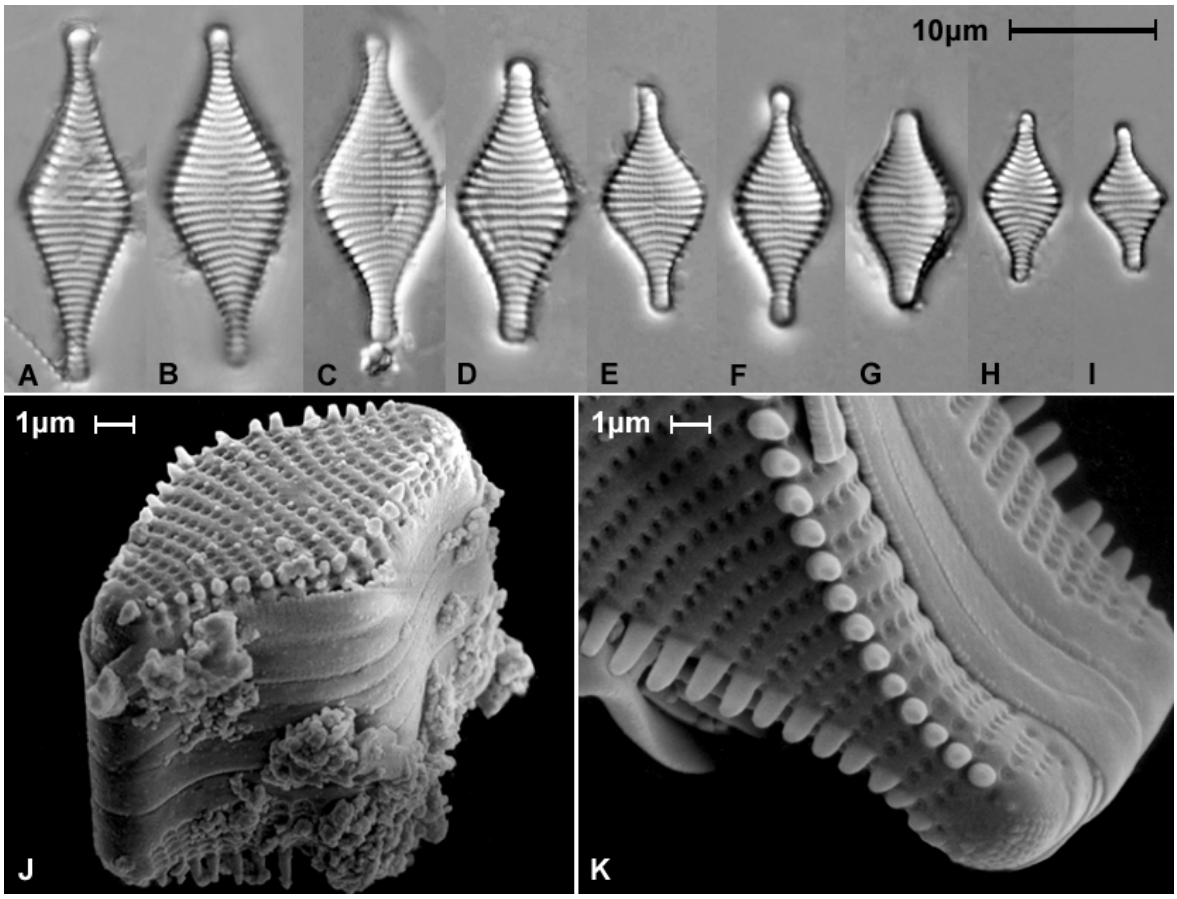


Figure VII.3 *Fragilariforma cassieae* from Clarence Lagoon, Tasmania. A-I, morphological progression during cell size reduction (LM); J, SEM of whole frustule; K, SEM showing detail of apex.

ETYMOLOGY: *Fragilariforma cassieae* is named after Dr Vivienne Cassie Cooper in honour of her outstanding contribution to diatom research in New Zealand.

HOLOTYPE CHR 565730. Material collected by C. Kilroy from Jordan Stream headwaters (Jordan Saddle, Canterbury, South Island, New Zealand), surface sediment samples from pool, 13 November 1999.

Isotypes: BM 101032; BRM Zu 5/43; CAS 221053; NIWA diatom collection, Christchurch, New Zealand (sample/slide #226).

COMMENTS: This species initially caught our attention because of the prominent areolae in many specimens, which under SEM are small poroids centred in round depressions (Fig. VII.1J). We examined populations of these diatoms (and similar forms, see below) from Jordan Stream (Figs VII.1, 2); Clarence Lagoon, Tasmania (Fig. VII.3); Deceit Peaks, Stewart Island (Fig. VII.4); Table Hill, Stewart Island (Fig. VII.5); Picone Lake, Tasmania (Fig. VII.6A-D) and Mount Kosciusko, Australia (Fig. VII.6E-H). In live material we have observed this species forming short zig-zag chains (Fig. VII.2) or occurring as isolated cells or in pairs. The Jordan Stream, Clarence Lagoon

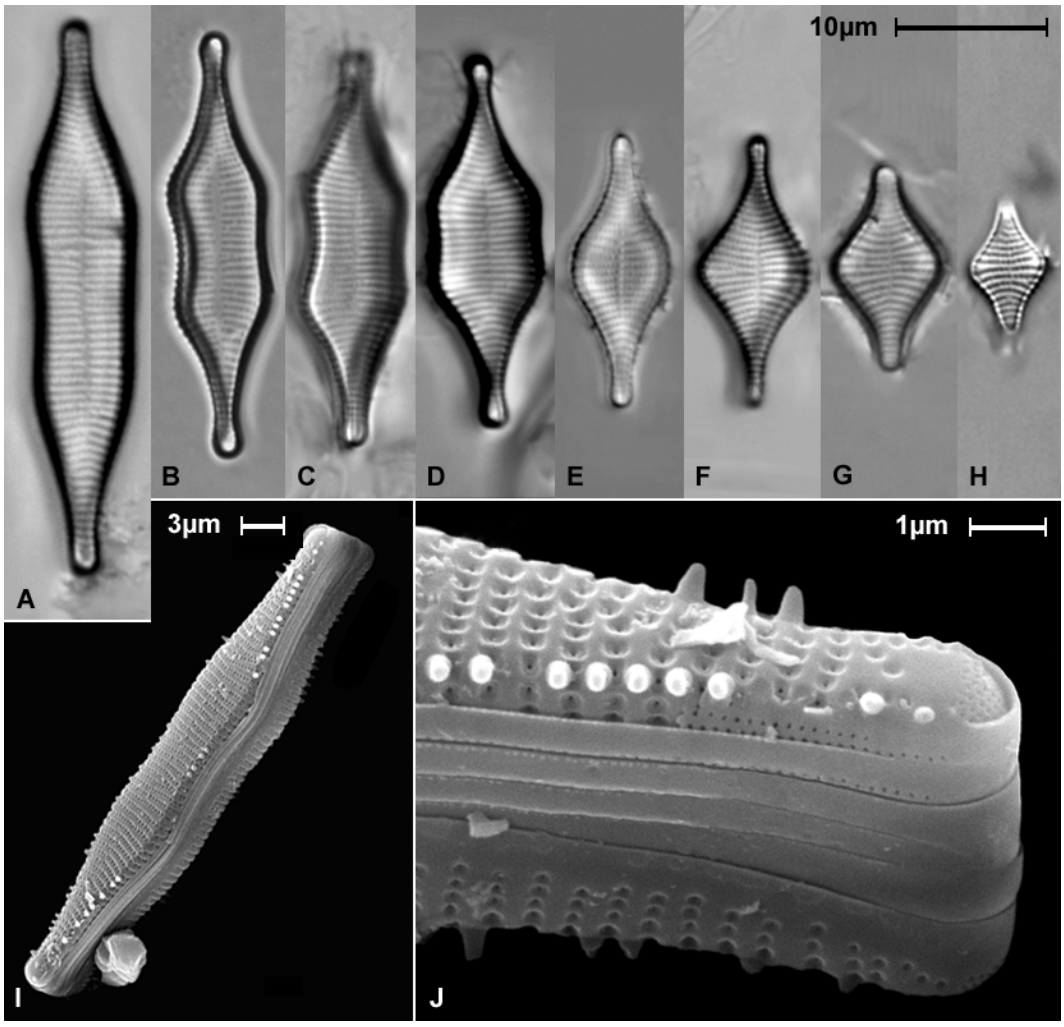


Figure VII.4 *Fragilariforma cassieae* forms from Deceit Peaks, Stewart Island. A-D, *F. cassieae* form 1 (LM); E, F, transitional forms; G, H, small cells, similar to the type population of *F. cassieae*; I,J, SEM showing whole frustule of *F. cassieae* form 1, and detail of the apex.

(Tasmania), Deceit Peaks and Mount Kosciusko populations had similar dimensions (Fig. VII.7), though areola density was more variable in the Jordan Saddle population than in the Tasmanian specimens in which almost all specimens had 28 areolae/10 µm. The irregular appearance of the largest specimen observed (27 µm long) in the type population suggests that it could be an initial valve (Fig. VII.1A).

In addition to the protracted-rhombic to rhombic *F. cassieae* valves present in the Jordan Saddle, Tasmanian and Mount Kosciusko samples, other, slightly different forms were observed in other localities. All the Stewart Island samples contained narrow, elongated diatoms, constricted at the centre of the valve, which possess ultrastructural features apparently identical to those of *F. cassieae* (Fig. VII.4A-D). These forms will be referred to as *F. cassieae* form 1. A peculiar feature of these constricted forms is that the valves tend to become wider during morphological

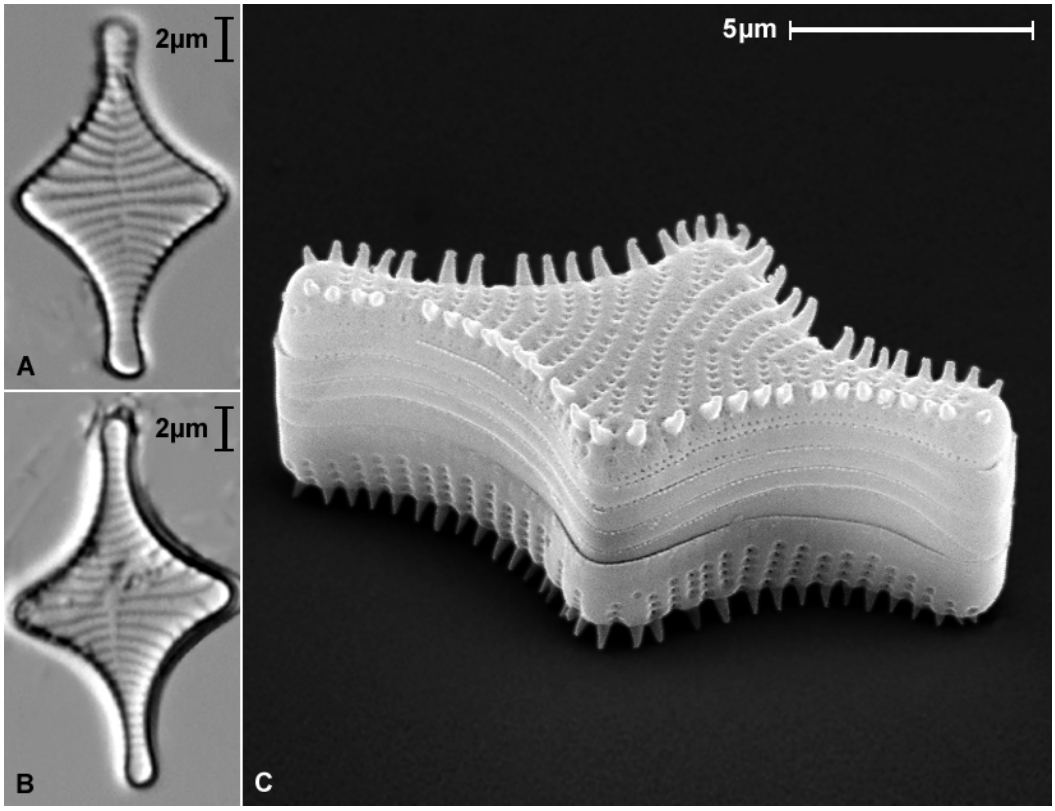


Figure VII. 5 *Fragilariforma cassieae* form 2, from Table Hill, Stewart Island. A, B LM; C. SEM.

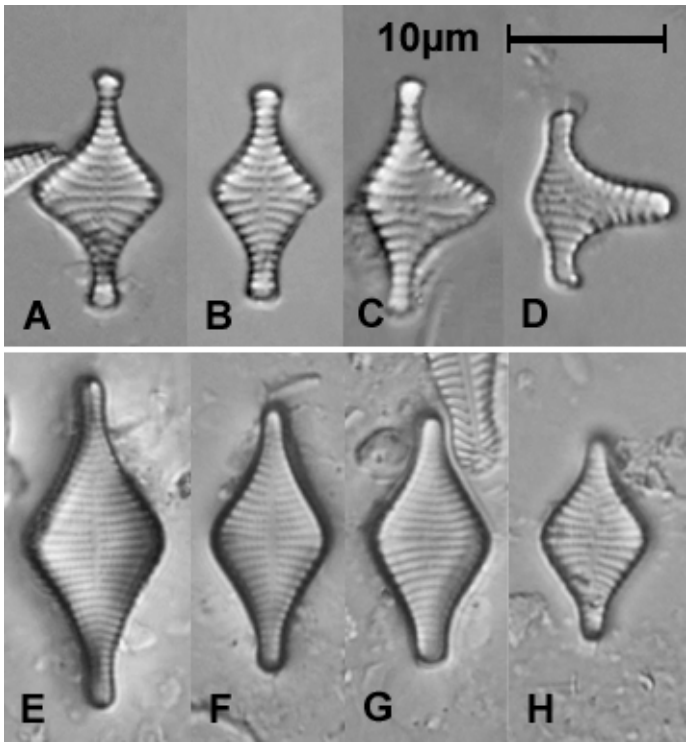


Figure VII. 6

A-D, *Fragilariforma cassieae* form 3, from Picone Lake, Tasmania. E-H, *Fragliariforma cassieae* from Mt Kosciusko, Australia.

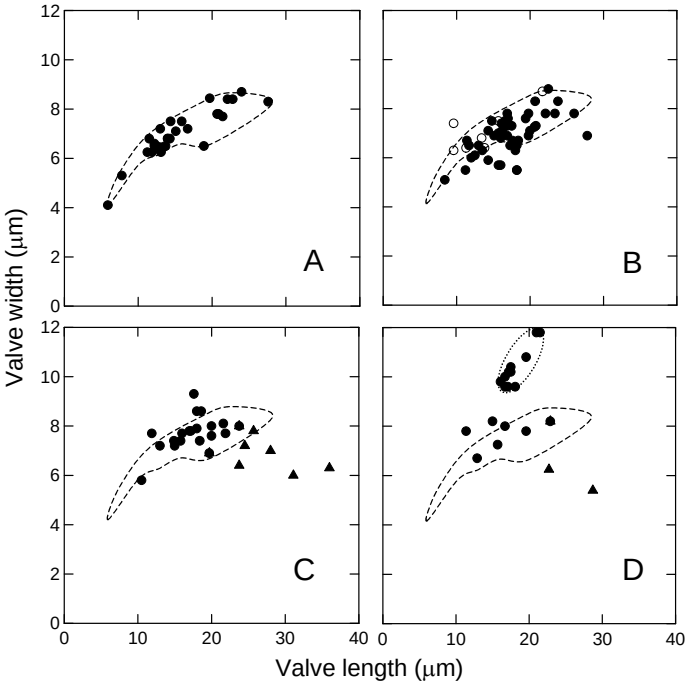


Figure VII. 7

Valve length versus width (measured at the widest point across the valve) for *Fragliariforma cassieae* and its forms. A, Jordan Saddle, Arthur's Pass (the type population). B, Australia: Clarence Lagoon. Tasmania (●) and Mt Kosciusko (○). C, Deceit Peaks, Stewart Island, constricted specimens (form 1) (▲) and protracted-rhombic (●). D, Table Hill, Stewart Island, constricted (form 1) (▲) and protracted-rhombic (●), with specimens of form 2 circled with a dotted line. The dashed enclosure on each plot represents the limits of the dimensions measured in the type population.

progression (Fig. VII.7C, D; see also F. *rakiuriensis*). Most non-constricted specimens from Table Hill, Stewart Island, were markedly wider than *F. cassieae*, with somewhat irregular striae (Fig. VII.5, 7D) and we refer to these as *F. cassieae* form 2. A third unusual population (*F. cassieae* form 3) was found in Lake Picone, Tasmania. These are all small, somewhat irregular in shape and often have isolated puncta in the central part of the valve (Fig. VII.6A-D). All these forms require further study and are discussed below. As their relationship with *F. cassieae* is as yet uncertain, we explicitly do not include them in the protologue of this species. Note that form here merely means a morphologically distinct form, and is not used in the formal taxonomic sense (ICBN 4.1).

Fragilariforma cassieae shares similarities with *Fragilariforma lata* (Cleve-Euler) Williams and Round, *Fragilariforma hungarica* var. *tumida* (Cleve-Euler) Hamilton, *Fragilariforma hungarica* (Pantocsek) Hamilton, and *Fragilariforma constricta* (Ehrenberg) Williams and Round. *F. cassieae* and the cruciform forms of *F. lata* are very similar in shape, dimensions and stria density (see Renberg 1977). Indeed *F. cassieae* was tentatively identified as *F. lata* by Vyverman et al. (1995). *F. lata* was described by Cleve-Euler (1953) as *Synedra parasitica* (W.Smith) Hustedt var. *genuina* Mayer f. *lata* Cleve-Euler. Only cruciform valves were described and depicted in the type description. We examined slides from the type locations named by Cleve-Euler (1953, p. 56), but only one specimen of (presumably) *F. lata* was located (Fig. VII.8A). However, there were many specimens of large constricted forms and these had proportions that differ from those of Stewart Island constricted specimens (see below). We therefore rely on the description of *F. lata* in Renberg (1977, cf. also Camburn and Charles 2000) for our comparison, which showed clear differences between the two species (Table VII.1). *F. cassieae* forms short zig-zag colonies (Fig.

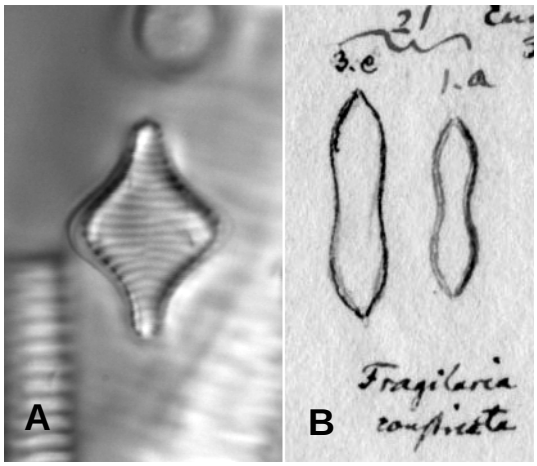


Figure VII.8
A, *Fragilariforma lata* (Cleve-Euler) Williams & Round, photographed from Cleve-Euler's material (slide S122588). Valve is approx. 12 μm long. B, *Fragilaria constricta* Ehrenberg, reproduced from Ehrenberg's original drawing sheet 2046. Note the lack of detail. (Drawing reproduced courtesy of Museum fur Naturkunde, Berlin, Germany. All of Ehrenberg's drawings are available for download from: http://www.museum.hu-berlin.de:55080/Ehrenberg/.)

VII.2) whereas *F. lata* occurs in "ribbon-like" colonies. Renberg (1977) stated *c*. 50 puncta in 10 μm for *F. lata*, whereas *F. cassieae* has 26–29 puncta in 10 μm. In contrast to *F. lata*, *F. cassieae* lacks spines at the apices but has well-developed pore fields at both apices. Thus, we conclude that *F. lata* and *F. cassieae* are two distinct species.

An illustration of *Fragilariforma hungarica* var. *tumida* (Cleve-Euler) Hamilton (as *Fragilaria hungarica* Pantocsek *var. tumida* Cleve) in Gasse (1978, pl. II, fig. 4) looks similar to *F. cassieae*, though the stria count given is somewhat higher (Table VII.2). The adjacent figure in Gasse (1978, pl. II, fig. 5) of *Fragilaria* aff. *hungarica* var. *tumida* A.Cleve corresponds very closely to our species, and Gasse (1978) noted strong similarity to *Fragilaria construens*. Close scrutiny of the illustration *suggests* prominent areolae, though a density is not given. A further illustration in Gasse (1986, pl. VI, fig. 1) identified as *Fragilaria hungarica* Pantocsek var. *hungarica* also resembles our species, though less convincingly. The illustration of *Fragilaria hungarica* Pantocsek in Mölder and Tynni (1970, fig. 20) also resembles *F. cassieae*. We therefore attempted to locate type material for both these taxa.

A thorough search of slides from the type locations named in Cleve-Euler (1953, p. 40) for *Fragilaria hungarica* Pantocsek var. *tumida* Cleve-Euler revealed no specimens that resembled her original illustration (Cleve-Euler 1953, fig. 349n). Therefore, we rely on the description and drawings in Cleve-Euler (1953) for her original concept of the taxon. The size range stated for *F. hungarica* var. *tumida* is within that observed for the protracted-rhombic valves in our New Zealand (Table VII.2), Tasmanian and Australian populations. The stria density is at the high end of our range. However, the fine ("zart"), parallel striae stated in Cleve-Euler's (1953) description of *F. hungarica* var. *tumida* are not consistent with *F. cassieae*, in which the striae tend to be radiate at the centre of smaller specimens and clearly punctate (Fig. VII.1D-H). Further, the shapes quoted and illustrated in Cleve-Euler (1953) do not correspond to the shape of *F. cassieae*.

Fragilaria hungarica var. *tumida* Cleve-Euler is listed and illustrated (LM) in several recent publications (Camburn and Charles 2000, Fallu et al. 2000, Kingston et al. 2001). It is clear that

Table VII.2 Comparison of selected features of *Fragilariforma cassieae* and *F. rakiuriensis* with the genus description for *Fragilariforma* and descriptions of closely related species.

	Colony formation	Plastids	Shape	Length (μm)	Width (μm)	Stria density (/10 μm)	Striae	Sternum/axial area	Location of spines	Pore fields	Reference(s)
***Fragilariforma* Williams & Round**	Straight or zig-zag	Several separate discs	Lanceolate–linear–elliptical, can be centrally constricted	-	-	-	Uniseriate extending across valve and onto mantle (but short of edge)	Very narrow or absent; occurs at some stage of life cycle	On interstriae on very edge of valve face	Simple, apical, extending onto valve face; densly packed areolae	Williams & Round 1987, Williams 1996a
***Fragilariforma cassieae* sp. nov.**	Zig-zag (observed)	Several separate discs	Rhombic with narrow protracted apices	11 – 24 (27)	6.2 – 9 (10.5)	15 – 18	Uniseriate, continuous across valve onto mantle (but short of edge); radiate in the middle in small forms	Narrow or absent, sometimes at centre only.	On interstriae at margin of valve face, not around ends	Apical, extending onto valve face, both apices; ~40 pores in close rows	This study
***Fragilariforma rakiuriensis* sp. nov.**	Linear?	Unknown	Lanceolate, constricted medially to rhombic, with narrow protracted apices	12 – 55	5.5 – 7.5	11 – 14	Uniseriate, irregularly parallel, continuous across valve and onto mantle (short of edge)	Usually absent, occasionally a break at the centre (in small forms)	On interstriae at margin of valve face, not around ends	None, but an area of small bumps at each apex (occluded pores?)	This study
***Fragilariforma lata* (Cleve-Euler) Williams & Round**	Straight, or solitary	Unknown	Oblong, deeply constricted medially to rhombic, with narrow elongated apices	4 – 35	3 – 9	15 – 17	Uniseriate, extending onto mantle, radiate in middle of valve face, parallel in larger forms	Absent or (often) very narrow	On interstriae at margin of valve face, around ends	None	Renberg 1977
***Fragilariforma hungarica* (Pantocsek)**	Unknown	Unknown	"Rhomboid – lanceolate"	19.2	6.6	17 – 18	Parallel, continuous to pseudoraphe along the whole valve length	Very narrow, linear	Unknown	Unknown	Pantoscek 1902

Hamilton											
***Fragilaria hungarica* Pantocsek var. *hungarica* (= var. *genuina*)**	Unknown	Unknown	"Rhomboid – lanceolate, straight edges, pointed ends"	20 – 25	6 – 8	17 – 18	Fine, parallel	Very narrow, linear	Unknown	Unknown	Cleve-Euler 1953
***Fragilaria hungarica* Pantocsek var. *tumida* Cleve-Euler**	Unknown	Unknown	Strongly rounded middle, somewhat blunt ends	15 – 20	6.5 – 10.5	18 – 20	Fine ("zart"), parallel	Not visible	Not around ends	Unknown	Cleve-Euler 1953
Fragilaria hungarica* Pantocsek var. *hungarica	Unknown	Unknown	Rhombic with wide protracted apices	20.6	8.3	15 – 18	Slightly radiate at centre of valve	Narrow linear	Unknown	Unknown	Gasse 1986 (pl. VI, fig.1)
***Fragilaria hungarica* var *tumida* Cleve-Euler**	Unknown	Unknown	Rhombic with protracted apices	20 – 28	9 – 11.5	17 – 19	Parallel, very slightly radiate at centre	Narrow linear	Not around ends	Unknown	Gasse 1978 (pl. II, fig.4)
***Fragilaria* aff. *hungarica* v. *tumida* Cleve-Euler**	Unknown	Unknown	Rhombic with narrow, protracted apices	12 – 16	9 – 10	15 – 16	Parallel	Very narrow, linear	"Distinct marginal spines" (transl. fr. French)	Unknown	Gasse 1978 (pl. II, fig.5)

their concept of *F. hungarica* var. *tumida* does not correspond to *F. cassieae*, particularly in the very blunt apices of the larger specimens. We therefore conclude that *F. cassieae* and *F. hungarica* var. *tumida* (Cleve-Euler) Hamilton represent different species.

Fragilariforma hungarica (Pantocsek) Hamilton was originally illustrated in Pantocsek (1892, pl. VIII, fig. 128) as *Fragilaria hungarica* nov. spec.; the accompanying description, which corresponds with (and refers to) the illustration in Pantoscek (1892), was published 13 years later in Pantocscek (1905, p. 53). However, a further illustration and description were named as *F. hungarica* n.s. in Pantoscek (1902, p. 79, pl. IX, fig. 226). The difficulty here is that the 1892/1905 illustration and description do not correspond to the currently accepted concept of *F. hungarica*, whereas the 1902 description and illustration do. Since the original, valid publication of *F. hungarica* (Pantocsek 1892) does not give enough details to allow unambiguous assessment of its identity (with respect to previously published fragilaroid species) (ICBN, Art. 42.3), and the 1902 description does, it would probably best to conserve the name *F. hungarica* for the latter, more usual concept of this species. Conservation would involve tracking down the original materials used for the 1892 and the 1902 publications. However, as neither of the Pantocsek illustrations resembles the new species discussed here, it is beyond the scope of this paper to resolve this problem. The discrepancy does not appear to have been noticed during or since the transfer of *Fragilaria hungarica* to the new combination *Fragilariforma hungarica* (Pantocsek) Hamilton (Hamilton et al. 1992).

The illustration in Cleve-Euler (1953) of *Fragilaria hungarica* α *genuina* closely resembles Pantocsek's (1902) illustration of *F. hungarica*. The accompanying descriptions differ slightly (Pantocsek (1902): 19.2 μm long, 6.6 μm wide, 17–18 striae/10 μm; Cleve-Euler (1953): 20–25 μm long, 6–8.6 μm wide, 17–18 striae/10 μm), both falling within the range of *F. cassieae*. However, the valve shape ("rhomboideo-lanceolatis") does not match that that of *F. cassieae*, which has a rhombic shape with narrow protracted apices in larger cells (VII.2) tending to a concave-rhombic to rhombic shape in small forms. In addition, the striae in *F. hungarica* are not distinctly punctate as in *F. cassieae*. We have been unable to locate any recent illustrations of *F. hungarica* other than those mentioned above and we can locate no scanning electron micrographs of *F. hungarica* or its varieties.

Scanning electron micrographs of *Fragilariforma constricta* in Williams and Round (1987) indicate that this species has areolae similar to those in *F. cassieae*. In addition, the stria density of the two species is consistent (Patrick and Reimer 1966, Krammer and Lange-Bertalot 1991) and the valve shape of *F. constricta* is quoted as "very variable" (e.g., Patrick and Reimer 1966). This variability is also discussed by Krammer and Lange-Bertalot (1991, p. 140–141) in relation to *F. lata* and *F. constricta* f. *stricta* (A.Cleve) Poulin. Nevertheless, no specimens, illustrations, or descriptions we have located of *F. constricta* and *F. constricta* f. *stricta* resemble *F. cassieae* or the related constricted form (see below) (for example, Ehrenberg's original drawings, sheet 2046 (Fig.

VII.8B); one of Wm. Smith's original slide mounts of *Fragilaria undata* Wm. Smith (syn. *Fragilaria constricta* Ehrenberg, as listed in VanLandingham 1967–1979); Cleve-Euler (1953), fig. 362a–g; Carter and Bailey-Watts (1981), pl. 8, fig. 40–43). Cassie (1989) identified *F. constricta* f. *stricta* as rare in a gypsum sample from an active volcanic area (White Island). We have been unable to locate any specimens in the original sample to check whether this diatom resembled any of our material.

ECOLOGY AND DISTRIBUTION: The type population (Jordan Saddle) was moderately common in sediment on an organic substratum in a pool in the headwaters of an exposed, sub-alpine, stream (altitude 1460 m), with pH 6.5–7.0 and water conductivity 31–52 μS cm^{-1}. We have no further water chemistry information at this stage. In Clarence Lagoon, Tasmania, the samples were also from sediment. Clarence Lagoon is a small, humic, dystrophic lake on dolerite bedrock with the optical properties of "corridor" lakes as described by Vyverman et al. (1995, 1996). *F. cassieae* form 1 was found at several localities throughout Stewart Island in sediment from slow-flowing streams or wet areas (Deceit Peaks, Table Hill, Rakeahua Valley) and in one small tarn (Little Mount Anglem). Water conductivity ranged from 65 to 105 μS cm^{-1}, the uncharacteristically high values for pristine, subalpine habitats in New Zealand being due to the influence of sea-water spray on surface freshwaters on the island. *F. cassieae* form 2 was present only in samples from Table Hill, Stewart Island. *F. cassieae* form 3 has been found in Lake Picone, Tasmania (pH 6.4, water conductivity 18 μS cm^{-1}).

In New Zealand, apart from the populations mentioned above, we have found isolated valves of *F. cassieae* in samples from Lake Hochstetter on the west coast of the South Island (M. Reid pers. comm.), from Goat Pass, Arthur's Pass National Park, and from the St Arnaud Range, northern South Island, suggesting a more widespread distribution. In addition a further population has been located in a pool in the headwaters of a stream (altitude ~1000 m) flowing from Bealey Spur, near Arthur's Pass, South Island (pH 6.85, water conductivity 22 μS cm^{-1}), approximately 7 km from Jordan Saddle.

***Fragilariforma rakiuriensis* C. Kilroy and K. Sabbe, sp. nov.** Fig. VII.9-10

Valvae cum signis principalibus ita ut communiter in genere *Fragilariforma*. Ab omnibus descriptis speciebus generis differt striis crassioribus, irregularibus, structura polorum cum spinis instructorum, areis porellorum indistinctis. Rimoportulae nullae. Plerumque sternum nullum.

Valves 11–55 μm long, (5.5) 6.5–9 μm wide, narrowly rectangular in girdle view. Cells forming linear colonies. Plastids unknown. 2 – 4 open girdle bands, each with a row of poroids on the edge facing the epitheca (can be partly obscured by overlapping of adjacent copula). In valve view, cells range from lanceolate, constricted in the centre of the valve, with distinctly protracted apices, to rhombic with narrow protracted apices. The transition from the constricted to rhombic forms occurs

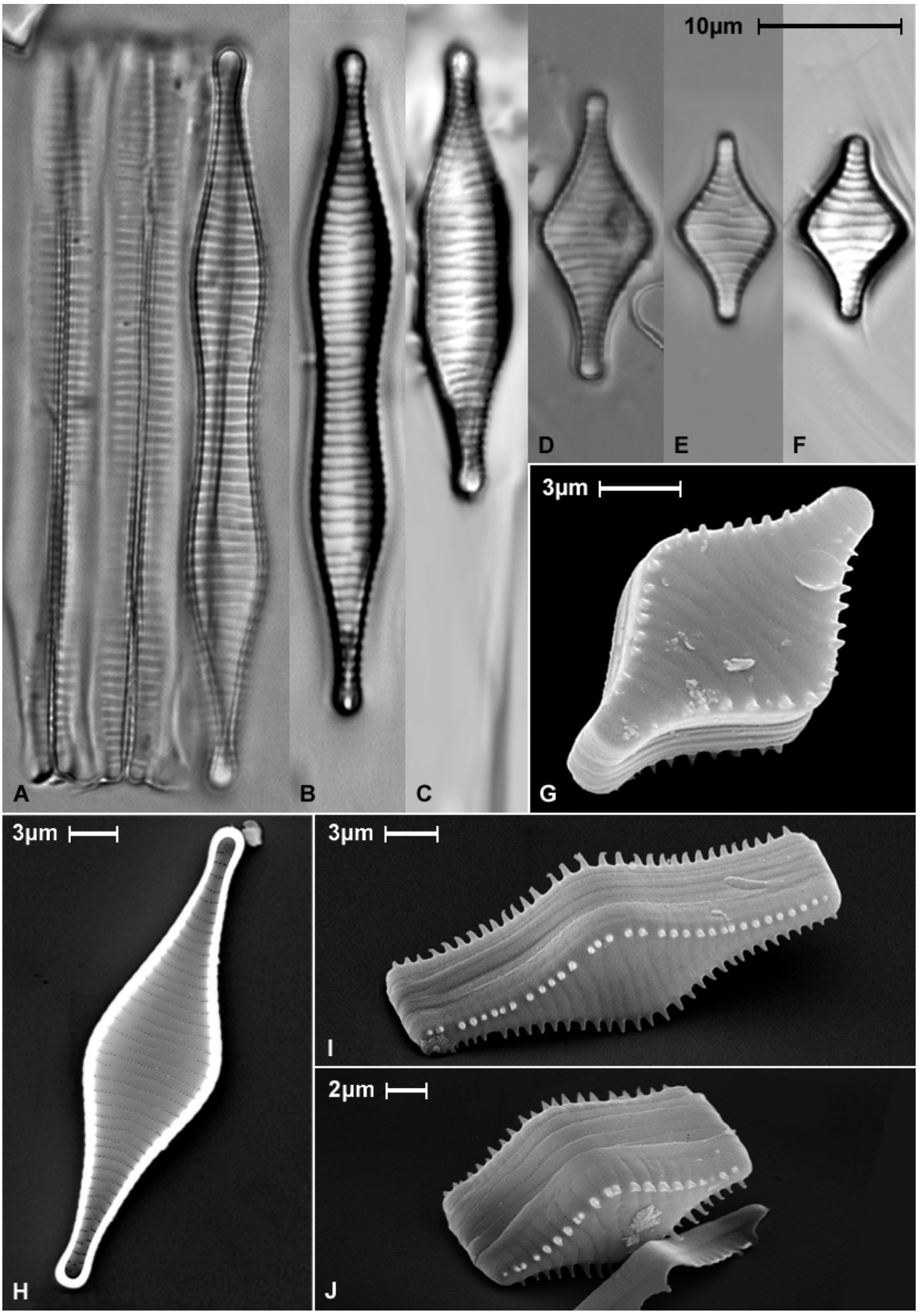


Figure VII.9 ***Fragilariforma rakiuriensis*** from the type population, Deceit Peaks, Stewart Island, New Zealand. A-F, morphological progression during cell size reduction (LM); G-J, SEMs of whole frustule (G) and valve interior (H) from the Deceit Peaks population, and frustules from Table Hill, Stewart Island (I, J).

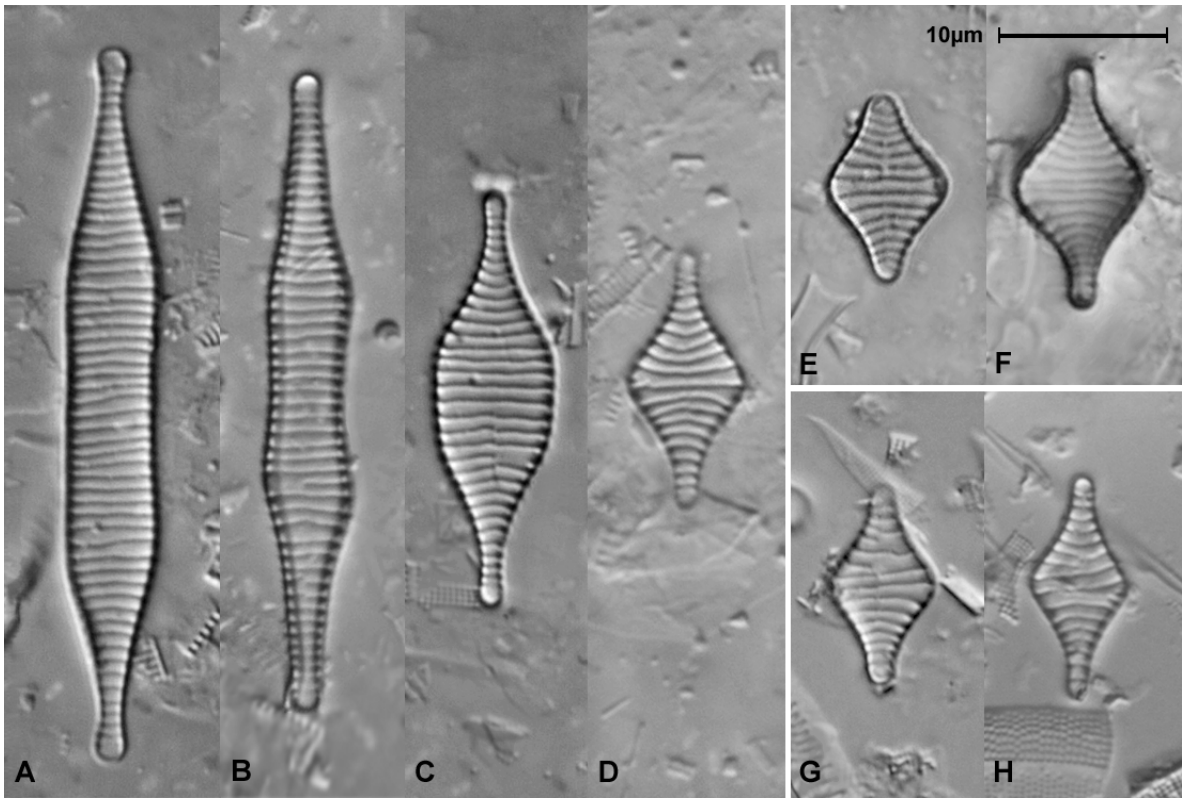


Figure VII.10 *Fragilariforma rakiuriensis* from locations in Australia: A-D, Sappho lake, Tasmania; E,F, Picone lake, Tasmania; G,H, Mt Kosciusko.

at about 22.5–29 µm long. Striae 11-14 in 10 µm, fine, continuous across the valve and over onto the valve mantle, more or less parallel but usually with an irregular appearance, axial break evident only occasionally; areolae not visible in LM. In SEM, areolae fine, 48–50/10 µm, and often occluded so that the external valve face is featureless except for slightly raised virgae. Internally simple small round openings. Rimoportula lacking. Marginal spines simple tapering hollow tubes on the interstriae, absent at the apices. An area of small bumps at each pole resembles an occluded pore field. Mantle plaques not usually present.

ETYMOLOGY: This species is named for one of the Māori names for Stewart Island (Rakiura), where the species was first recognised. Rakiura translates as “land of the glowing skies”, possibly a reflection of the visibility of the Aurora Australis in the area.

HOLOTYPE: CHR 565732. Material collected by Matt Charteris, from a stream on Deceit Peaks, Stewart Island, New Zealand, 10 November 1997.
Isotypes: BM 101033; BRM Zu 5/44; CAS 221054; NIWA diatom collection, Christchurch, New Zealand (#A6).

COMMENTS: We have examined populations of this species from three localities on Stewart Island (Deceit Peaks (the type population), Table Hill, and Little Mount Anglem) (Fig. VII.9). *F. rakiuriensis* was moderately common in some samples examined, although the valves in cleaned material were difficult to examine as the frustules often remained intact and were visible only in girdle view. We have also examined specimens from Tasmania (Fig. VII.10A-F), where it is relatively widespread (Vyverman et al. 1995, as *Fragilaria constricta* f. 1 and f. 2, pl. 16, figs 14–22, 11–13 str/10 μm), and from mainland Australia (Mt Kosciusko, Fig. VII.10G,H). We have been unable to examine live material from any location, but under LM we have observed the constricted frustules joined in short linear chains (e.g., Fig. VII.9A). Like *F. cassieae*, the small basically rhombic cells resemble *Staurosira construens* Ehrenberg in overall shape and size. However, ultrastructural features (particularly the structure of the areolae and copulae) place this new species within *Fragilariforma*. It is separated from *F. lata*, *F. hungarica*, *F. hungarica* var. *tumida*, and *F. cassieae* by its lower stria density (only 10–14 striae per 10 μm), somewhat irregular striae, and lack of an axial area in most specimens. Further differences are summarised in Table VII.2. The areola density corresponds to that of *Fragilariforma lata* but the puncta are usually completely occluded externally or visible only as tiny poroids (Fig. VII.9G,I,J). As in the larger, constricted *F. cassieae* form 1 (see above), the valves of the larger, constricted forms of *F. rakiuriensis* increase in width during the vegetative cell size reduction cycle so that the widest dimension of even the smallest cruciform cells generally exceeds that of the constricted forms (Figs VII.9, 11). This phenomenon is discussed in detail below.

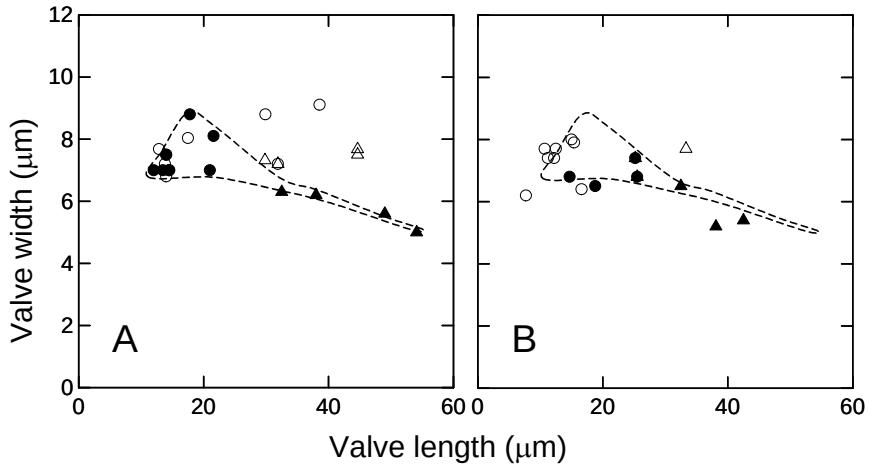


Figure VII.11 Valve length versus width (measured at the widest point across the valve) for *Fragilariforma rakiuriensis*. A, Stewart Island: the type population, Deceit Peaks (filled symbols) and other locations on Stewart Island (open symbols). B, Australia: Tasmanian populations (filled symbols) and specimens from Mt Kosciusko (open symbols). ●,○, protracted-rhombic; ▲, △, constricted. The dashed enclosure on each plot represents the limits of the dimensions measured in the type population.

ECOLOGY AND DISTRIBUTION: Specimens found so far have come from both running and still water habitats. The type population was collected from an open, rocky stream at 500 m altitude in Deceit Peaks, Stewart Island, with a reported pH of 5. For the Table Hill, Stewart Island, samples, water conductivity water was c. 100 μS cm^{-1} and pH was 5.2–5.6 in both flowing and standing water in the vicinity of the sample locations. In Tasmania, *F. rakiuriensis* mainly occurs in the western lakes, which are dystrophic, acidic, with high Gilvin values and an ionic composition close to that of seawater. (For more details on the Tasmanian lake provinces, see Vyverman et al. 1996.) For example, it is one of the dominant diatoms in Sappho Lake (pH c. 6.1, water conductivity 16 μS cm^{-1}). To date, *F. rakiuriensis* has been reported only from Stewart Island and Australia, and possibly from Lake Hochstetter, South Island, New Zealand (M. Reid pers. comm.).[1]

Discussion

Under LM, cells of *Fragilariforma cassieae* and *F. rakiuriensis* share the same rhombic shape with narrow, protracted apices, and have almost identical dimensions and size range. However, *F. cassieae* and *F. rakiuriensis* are clearly separated on the basis of stria density, and the fact that in *F. cassieae* the areolae are usually distinguishable under LM.

The characters that separate *Fragilariforma* from other genera formerly placed in the genus *Fragilaria* (Williams and Round 1987, 1988) are striae arrangement, girdle band construction, and plastid shape. Both *F. cassieae* and *F. rakiuriensis* correspond to *Fragilariforma* on the basis of the first two characters (see Table VII.2), and the third for *F. cassieae* (plastid shape is unknown for *F. rakiuriensis*). Williams (1996a) elaborated on the consistent appearance of a faint central sternum at some point in the life cycle and the use of this feature as a diagnostic generic character. Both our new species conform with this character. In *F. cassieae*, an axial area bisecting the valve is seen in specimens of various sizes (e.g., Fig. VII.1A,C,E); in *F. rakiuriensis* the feature is much less common but discernible in some specimens (e.g., Fig. VII.9E). In the original description of the genus (Williams and Round 1987) the presence of a single rimoportula is also noted. Both new species lack a rimoportula, but other species placed in *Fragilariforma* may either lack this character (e.g., *F. lata*) or possess it in occasional specimens only (e.g., *F. platensis*, see Williams (1996a)). While the possession of one or more rimoportulae may be used as a generic character (for example, in *Eunotia*), exceptions do not necessarily preclude species from a genus. Round and Williams (1992) mentioned this in relation to a commentary (Lange-Bertalot 1989) on the establishment by Williams and Round (1987) of several new genera based on *Fragilaria*. For example, *Eunotia triodon*, unlike all other known *Eunotia* species, lacks a rimoportulae, but on the basis of other characters is clearly a *Eunotia*. Likewise, rimoportulae are facultatively present in the genus *Eunophora* (Vyverman et al. 1998). As Round (1996) pointed out "… it is the presence of a

[1] Note than a few valves of this species have since been found in samples from the Bealey wetland area.

set of structural features which defines the genus. The set of features may have minor variation and sensible judgement is always a vital aspect of taxonomy!" On the basis of the features mentioned above we are confident that *Fragilariforma* is the appropriate genus for the two new species.

The prominent, widely spaced areolae in *F. cassieae* are not inconsistent with the generic character of "areolae small, circular, with an external, simple plate-like velum with a single central opening" (Round et al. 1990). The vela are simply larger and therefore more evident. Other *Fragilariforma* species possess the same areola structure, including *F. strangulata* and *F. constricta* (Williams and Round 1987), whereas *F. lata* apparently has no outer depression surrounding each poroid (see Renberg 1977).

All populations of *F. rakiuriensis* studied contained both small, basically rhombic valves with narrow, protracted ends and longer, constricted cells. The changeover from constricted to rhombic occurs at 22–29 μm. A feature of the size progression in the *F. rakiuriensis* constricted cells (and also in the constricted *F. cassieae* form 1, see below) is that the shorter cells can be considerably wider than the longer ones (Fig. VII.11). Round (1972) noted that in many pennate diatoms, particularly needle-shaped frustules such as *Synedra* and *Nitzschia* species, a reduction in length is not necessarily accompanied by the same reduction in width. He suggested that an increase in size, or at least no decrease, could be due to greater flexibility of the girdle bands at the middle of the valve than at the apices. Hustedt (1930) commented that some elliptical/elongate diatom species actually increase their transapical axis with cell division. More recently, Mann (1994) reiterated that the diatom cell wall can have some flexibility and, in diatoms whose girdle bands are curved enough, the daughter cells may be larger (wider) than the parent cells. Marked changes in valve shape through successive cell divisions occur in other species of *Fragilariforma*. Renberg (1977) illustrated a succession of cell shapes through size reduction in *F. lata*, with the shorter cells apparently slightly wider than the longer bi-undulate forms. In their recent study of *Fragilariforma* taxa, Kingston et al. (2001) showed the same phenomenon in morphological series of *Fragilariforma constricta* var. *trinodis* and *Fragilariforma polygonata*. In none of these examples is the width expansion with cell reduction quite as striking as in *F. rakiuriensis* and *F. cassieae* form 1. However, as in the other *Fragilariforma* species described by Renberg (1977) and Kingston et al. (2001), both the protracted-rhombic and constricted valves of *F. rakiuriensis* seem to belong to the same species. For *F. cassieae* and its morphological forms, the situation is more complex.

In the type population of *F. cassieae* from Jordan Saddle, South Island, New Zealand, and populations from Tasmania, we have observed only rhombic cells with narrow, protracted apices, including forms that appear to be initial cells (Fig. VII.1A). This is in spite of a thorough search of samples and repeated collections over three years from the type location. Constricted forms (*F. cassieae* form 1) were present only in the Stewart Island localities and in the sample from Mt Kosciusko. The progression from constricted to rhombic was particularly evident in the specimens

from Deceit Peaks (Fig. VII.4), where the smaller frustules had shape and dimensions similar to those of the type population of *F. cassieae* (Fig. VII.7A,C). The most likely explanation is that the constricted *F. cassieae* form 1 forms part of a continuum with the protracted-rhombic specimens from this locality (see, for example, Fig. VII.4E,F, which appear to be transitional forms). This would imply that in both the South Island and Tasmania size reduction in *F. cassieae* has progressed beyond the constricted/protracted-rhombic transition range, and sexual reproduction has not occurred recently. This is not unlikely as diatom life cycles (and hence size restoration through auxosporulation) can last anything from 2 to 20 years (Mann 1988). This problem is also highlighted by Mann (1999), who commented "if one population is sampled soon after auxosporulation, and another is caught close to the minimal size, it can be a matter of guesswork whether they belong to the same taxon." Therefore, we cannot completely rule out the possibility that typical *Fragilariforma cassieae* and *F. cassieae* form 1 are actually two distinct species, and that the latter forms a continuum with the protracted-rhombic cells from the same localities. Indeed, the length of the longest rhombic (initial?) valve observed in the type population (27 μm) of *F. cassieae* was greater than the length of transition to protracted-rhombic valves (ca. 22.5 μm) observed in the Deceit Peaks populations. The strong similarity between the protracted-rhombic specimens from the Jordan Saddle population and from Deceit Peaks could be then explained by the fact that during size reduction, some *Fragilariforma* species that are clearly separated in their larger forms become indistinguishable (Kingston et al. 2001). Thus, Kingston et al. stated: "Our observations of *F. hungarica* var. *tumida* lead us to conclude that it is very difficult to separate from small specimens of *F. polygonata*." Clearly, further sampling and detailed examination of live populations from both the type locality and Deceit Peaks (both *in situ* and in culture) are required to obtain a definitive answer to this problem. In the meantime, in this paper we describe the species *F. cassieae* with a size progression as illustrated for the Jordan Saddle population and that in Clarence Lagoon, Tasmania (Figs VII.1A-I, 3A-I) and acknowledge that further investigations are required to establish the status of the Deceit Peaks population.

In another Stewart Island population (sample 327 from Table Hill), almost all the protracted-rhombic cells are markedly wider than those of the type population (*F. cassieae* form 2, Figs VII.5; 7A,C), but the constricted forms from that locality resemble those of the Deceit Peaks population (Figs VII4; 7D). Again, it is difficult to comment on the significance of this since the number of valves observed was quite small. Further work is necessary to establish whether this shape variation represents a response to environmental conditions, or whether this morphotype is genetically distinct from the other Stewart Island forms. Likewise, the significance of the small-celled *F. cassieae* form 3 from Picone Lake (Tasmania) (Fig. VII.6A-D) needs further study before its relationship with typical *F. cassieae* can be assessed.

Many species of *Fragilariforma* appear to be characterised by a preference for acidic waters (e.g., *F. lata*, *F. acidobiontica*; see Table VII.1). This is not the case for the populations of *F. cassieae* identified so far (pH 6.7–7 for the type population), though it may apply to *F. rakiuriensis* on Stewart Island (pH 5–5.6). Interestingly, the *F. cassieae* forms from Stewart Island also inhabit these more acid locations. Further work is required to determine whether this represents a habitat preference that may be important in distinguishing *F. cassieae* from the Stewart Island forms.

Our work on the present group of species contributes to a growing opinion that endemism in freshwater diatoms, particularly based on Southern Hemisphere locations, may be much more common than was previously thought (e.g., Mann and Droop 1996, Mann 1999, Kociolek and Spaulding 2000, Kociolek and Stoermer 2001). Early diatomists in New Zealand such as Barber (1962) commented on the fact that the diatom flora of even relatively remote places such as Cass (central Canterbury foothills, South Island) were mostly European (British). Foged (1979) mentioned a treatise on diatoms from Otago, South Island (Lindsay 1867), in which the author registered 110 freshwater diatoms and emphasised that 90% were “British forms” and that many were cosmopolitan. Even in rather specialised habitats such as thermal areas, which might be expected to harbour a higher proportion of endemics, Cassie (1989) reported only four endemic diatom taxa out of 144 identified. However, recent taxonomic work on selected diatom taxa from relatively pristine areas, particularly alpine tarns and seeps, has led to the recognition of an increasing number of endemic taxa in the freshwater diatom flora of New Zealand and the Australasian region (e.g., Vyverman et al. 1998, Sabbe et al. 2001 and references therein, R. Lowe unpublished data).

In relation to Southern Hemisphere endemism, a further consideration is whether the distribution of these species of *Fragliariforma* might extend to other parts of the Southern Hemisphere than New Zealand and Australia. New Zealand and Tasmania already share one very distinctive genus, *Eunophora* Vyverman, Sabbe and Mann. Vyverman et al. (1998) reported that *Eunophora* species were abundant in some Tasmanian lakes, and had also been identified from a few locations in New Zealand. Since then, the genus has turned out to be extremely common in New Zealand, occurring from lowland wetland areas to subalpine tarns, in North, South and Stewart Islands (W. Vyverman, K. Sabbe, C. Kilroy and R. Lowe unpubl. data). Yet, to our knowledge, it has turned up nowhere else in the world. The two locations also share at least two species of *Actinella* (Sabbe *et al.* 2001). Both *F. cassieae* (and its related forms) and *F. rakiuriensis* are much less conspicuous than *Eunophora*, and also less common. But , apart from the populations found in a sample from Mt Kosciusko, they also do not seem to be represented in other parts of Australasia and the Pacific (e.g., Foged 1978, Vyverman 1991, Moser et al. 1998), or in South America (e.g., Rumrich et al. 2000).

In a review of the importance of undertaking ecological investigations on diatoms in parallel with taxonomic studies, Kociolek and Stoermer (2001) suggested that microbial floras could be used for defining "natural" habitats that are worthy of conservation. The type locations of both *F. cassieae* and *F. rakiuriensis* are in protected Conservation Estate in New Zealand, areas that have already been identified as having special values, and are in isolated locations that are likely to contain additional undescribed endemic species of diatoms. Recent work has re-emphasised the importance of accurate diatom identifications if these organisms are to be used as indicators of past and present changes in aquatic ecosystems (Morales et al. 2001). Thus, careful definition of endemic (at least to the Australasian region) diatom taxa, such as *F. cassieae* and *F. rakiuriensis*, is a step towards improving the potential for use of diatoms as indicators, in addition to contributing to a more complete picture of diatom biodiversity in New Zealand.

3. Synthesis and conclusions

Below I present a summary of and conclusions from my findings in relation to each of the research questions (Introduction, section 1.6, pp. 14 – 17). References to the literature are made sparingly: for details refer to the relevant manuscripts (Original papers 2.I to 2.VII, and as listed in the Introduction, section 1.7, pp. 14 – 17), which are referred to below using roman numerals. Also included is a brief discussion of further questions that arose during the course of the work.

3.1 Patterns of endemism in benthic freshwater diatoms in New Zealand [I]

Is there any pattern to the occurrence of endemic freshwater diatom taxa in New Zealand, in terms of the habitats in which they are found, and can this be reconciled with existing ecological theory?

Reports of diatom taxa assumed to be endemic in New Zealand, or within the New Zealand - Tasmania - Eastern Australia bioregion (see Introduction, section 1.4), have appeared periodically in the literature (e.g., Schmidt et al. 1874 – 1959, Foged 1979, Kociolek and Stoermer 1988). Recent descriptions have included the new genus *Eunophora* (Vyverman et al. 1998), new species of *Actinella* (Sabbe et al. 2001), and new species of *Fragilariforma* [VII]. While the general ecological conditions required by each taxon are known from observations on their habitats, it is difficult to draw conclusions about overall habitat patterns without undertaking a new analysis. Ideally such an analysis should be undertaken in the context of a predictive theory, which would provide some *a priori* explanation for expected patterns. Since ecological theory relating to diatom distributions predicts ubiquity (Finlay et al. 2002), then hypotheses formulated using other organisms must be considered. A simple model to predict endemism in plants can be derived based on the concepts developed for the Dynamic Equilibrium Model (DEM, Huston 1994) [I]. According to the model, which was based mainly on observations on *terrestrial* plants, highest proportions of endemic plant taxa are most likely in low disturbance, low productivity environments, though some may also be expected in low productivity environments across the entire range of disturbances.

To test this model for diatoms, I undertook a landscape-scale analysis of diatom communities throughout New Zealand, in a three-step process. First, I determined the proportion of endemic diatoms (using biovolume estimates) in >320 benthic diatom samples representing diatom communities from sites covering the entire range of freshwater habitats (except warm/hot springs[2]). The samples were from a diatom collection accumulated over the past five years. Second, using

[2] Hot springs were not included in the analysis because of insufficient samples.

existing national databases of climatic, hydrological, geological and landuse data,[3] indices of relative productivity and disturbance were derived for each site. Third, conformity to the model was tested by examining relationships between proportions of endemism and both disturbance and productivity indices, with the model predicting negative correlations in both cases.

It should be noted that disturbance in this analysis was interpreted in the physical sense (e.g., as defined in Reynolds 1993; Biggs et al. 1998a) rather than the traditional biological sense (i.e., any disruption that results in loss of individuals or populations, as defined, for example, in Huston, 1994). The physical definition avoids circularity and allows clear separation of the effects of disturbances and productivity. The present model extends a conceptual model proposed by Biggs et al. (1998a,b) for predicting periphyton biomass and community composition in New Zealand streams and rivers from the habitat characteristics of disturbance regime and resource supply (productivity).

I found that the diatom data approximated the DEM model predictions. There was a statistically significant negative relationship between endemism and disturbance, but not between endemism and productivity. In his original discussion, Huston (1994) indicated that the most important environmental attribute for maintenance of endemism was low productivity. The empirical data suggest that low disturbance is more critical for freshwater diatoms. The discrepancy is attributed to differences in human-induced disturbance patterns in terrestrial and aquatic environments.

A further important outcome of this analysis was that high altitude tarns and bogs (mire pools), appeared to harbour the highest proportions of endemism in diatoms (compare Figures I.1b and I.1c in [I]). Endemism was also prevalent in some North Island spring / seep habitats. Nevertheless, the analysis confirmed that New Zealand's diatom flora – on the basis of morphological discrimination of species – comprises predominantly cosmopolitan taxa. Note that the degree of endemism in the analysis was calculated as proportion of diatom biovolume made up of taxa classified as endemic or potentially endemic (I, and see Introduction, section 1.5), rather than numbers or proportions of endemic diatom taxa. This approach was taken because each sample represented the community in a single local interaction neighbourhood (e.g., see Melbourne et al. 2007). At this scale *individuals* are important and it appears more relevant to measure the success of endemism using the proportions of individual diatoms with restricted range sizes rather than aggregating them into species. I considered the proportions of endemism in terms of species numbers in a separate analysis comparing the effects of scale on assessments of coexistence (see Section 3.3, below). In

[3] Note that this landscape-scale analysis would not have been possible without the use of a national GIS database of environmental data. The framework for the databases is the River Environment Classification (REC), which is a hierarchical system of categorical information applied to all mappable river segments (scale 1 : 50 000) throughout New Zealand (Snelder and Biggs 2002). The REC comprises approximately 565 000 individual river segments (i.e., river reaches between tributary junctions), with an average resolution of 750 m. GIS layers of continuous environmental data (Leathwick et al. 2003) have been applied to the REC network, which provide descriptions of conditions in individual reaches in unprecedented detail. Both reach-specific and integrated upstream-catchment data are available.

terms of species numbers in the present analysis, I classified over 10% of taxa as either endemic or likely to be endemic (i.e., undescribed taxa that were either similar to species already described only from Tasmania and / or eastern Australia, or distinctive and not known from any other location). A further 22% were considered to be possibly endemic on the basis of consistent differences from similar Northern Hemisphere taxa. Compare these proportions with the 2.3% currently assessed as endemic by Harper (in press).

I concluded from this analysis that, in broad terms, the distributions of endemic diatoms in New Zealand conform to predictions derived from observations on terrestrial plants. This suggests that dispersal-limitation *does* play a role in determining the range sizes of diatoms (as it does in higher plants), and that ubiquity is not a general rule. If ubiquity in diatoms were the general rule, then the outcome of the analysis would have been expected to be (1) a much lower proportion of species classified as endemic, and (2) restriction of these species to highly unusual habitats that are rare or absent elsewhere. Globally, high-altitude (or high-latitude) tarns and mire pools are certainly not rare habitats, particularly the latter, which have attracted considerable research in the Northern Hemisphere (see III for numerous references). In addition, other known endemic species such as *Rhopalodia novae zealandiae* and *Gomphoneis minuta* var. *cassieae* occur in large oligotrophic lakes and low-nutrient rivers respectively, neither of which are unusual habitats. Species found in stable environments in higher productivity areas included an unusual, undescribed species of *Melosira* (or possibly *Pseudopodosira*) in a sandstone rock seep. Another unusual, possibly endemic, species (*Frankophila biggsii* Lowe) has recently been described from a limestone rock seep in South Island (Lowe et al. 2006). This species was not included in the present analysis, but further illustrates the potential for stable environments to maintain populations of endemic diatoms.

As emphasised in the Introduction, section 1.5, the conclusion from this analysis [I] is contingent upon accurate and consistent identification of diatom species. In the present analysis all species were scrutinised in comparison with the available literature, and voucher specimens (slides) have been retained for future reference.

3.2 Tarn / mire pool environments and endemic diatom taxa [II, III, VI, VII]

What is it about tarn/mire pool environments that allow them to support high proportions of endemic and unusual taxa?

The analysis used to address my first research question (see Introduction, section 1.6) confirmed that tarns / mire pools appear to be especially favourable habitats for the maintenance of endemic diatom taxa. According to the conceptual model [I] this can be attributed to the low disturbance, low productivity conditions prevalent at such sites. However, the landscape-scale approach to testing the model does not permit examination of the specific responses of taxa to environmental variables. The remainder of this study therefore comprised more detailed studies in a single,

representative study area: a system of shallow pools and tarns in a peat-based wetland area (a mire) containing *Sphagnum,* among other species, at about 1000 m altitude on the northern flank of Bealey Spur, near Arthur's Pass, Canterbury (refer to II for a detailed description of the study area, including a map). Preliminary collections had shown high proportions of at least two endemic taxa (*Eunophora* species) at some sites. I conducted two separate studies at the Bealey study site to address the second question.

In the first study [II], I investigated whether environmental variation over the study area could be related to the local distributions of diatom taxa, especially the two species of *Eunophora*. From this I hoped to define the preferred habitat of *Eunophora* and other species more precisely. Benthic diatom community composition was determined at 20 sites throughout the wetland, along with a suite of environmental variables, including water pH, conductivity, and major dissolved nutrients and ions. Water depth was standardised and all samples were collected in the same way from pools with similar soft, organic substrate, dominated by Cyanobacteria. I also assessed the community composition of other major algal groups in each sample.

The analysis showed that diatom community composition was strongly associated with water pH and less strongly with conductivity and g440 (a measure of water colour arising from dissolved humic acids). No other parameters, including abundances of other algal groups, showed overall correlations with diatom community composition. Narrow pH tolerances in diatoms are well known (Batterbee et al. 1999). In the present study, the strength of the association over such a small area (approximately 7 ha) and pH range (5.1 – 6.8) was surprising. Several individual diatom species showed strong correlations with pH, occurring in high relative abundances at sites near their pH optima, but at low abundances or absent elsewhere. However, relative abundances of both species of *Eunophora* were unrelated to pH and all other measured parameters. Further, the pH ranges in which the two species occurred in the present study did not correspond to those found for the same species in Tasmania (Vyverman et al. 1998). This meant that the analysis raised more questions than it answered [see II, Discussion]. Nevertheless, it also showed that a high proportion of the diatom taxa in the study area did not correspond to known cosmopolitan diatom species, including several distinctive taxa [VI, VII].

It was interesting that I found low abundances of the endemics *Fragilariforma cassieae* and *F. rakiuriensis* in a small proportion of the Bealey samples. (These were among the species that prompted this study initially.) Their formal description [VII] supports the growing recognition of the endemic component of the New Zealand freshwater diatom flora.

Detailed examination of 28 species that made up the bulk of the diatom community at the Bealey study site (in both numerical and biovolume terms) has shown that nine taxa were morphologically indistinguishable from known species with cosmopolitan distributions. For a further five taxa, a cosmopolitan distribution appears very likely on the basis of close morphological similarity to known species, and is therefore assumed for the purposes of the

analyses. For two further species, information is lacking at present, or the literature is inconsistent or ambiguous, therefore these were assigned “undetermined” status. Three species are certainly endemic (under the definition presented in the Introduction, section 1.4): two species of *Eunophora*, and *Frustulia cassieae* Beier and Lange-Bertalot. Finally, nine appear to represent undescribed species that are assessed as being very likely endemics. For a summary of the taxonomic results, see Table VI.1. Thus, the detailed taxonomic analysis confirmed the high level of endemism in these environments (>42% of the most common taxa are either endemic or undescribed likely endemic).

With respect to the very distinctive genus *Eunophora* – but also to other endemic taxa – one question raised was: are these species confined to New Zealand (and sometimes Tasmania) because these are the only locations worldwide where suitable conditions exist for populations to thrive? I addressed this in the second study related to my second research question by examining environmental conditions over time at four sites in the study area, and drawing comparisons with equivalent data from overseas [III]. The four sites were selected using existing data [II], to represent a gradient of pool types over the study area.

A two-year dataset of multiple physical and water chemistry parameters showed inconsistent seasonal differences among the pools, which could be explained by ombrotrophic vs. minerotrophic water sources, and pool size. For example, winter minima in water pH and g440 did not occur at all four sites. There were also inter-pool differences in relationships between chemical and physical parameters. In many cases, relationships were consistent with those identified in mire systems in Northern Europe. However, in a comparison of gradients of calcium vs. pH, which has been used as the basis of mire classification in Northern Europe (e.g., Wheeler and Proctor 2000, Sjörs and Gunnarsson 2002), I found much higher pH in the Bealey mire pools relative to Ca concentrations compared to Northern European datasets. Other data from New Zealand fell on the same trajectory as the Bealey data, as did data from Tasmania. Water chemistry differences between New Zealand and Northern Europe may be attributable to a combination of rainfall chemistry differences between the two regions (e.g., Verhoeven et al. 1987), vegetation differences (e.g., McQueen and Wilson 2001), and high rainfall throughput (e.g., Worrall et al. 2002). Vegetation type and high rainfall may contribute to unusually low levels of DOC in the pools assumed to be ombrotrophic (less than one-third of the world median for bog waters). Low DOC implies low levels of organic acids, which normally lead to low pH levels in ombrotrophic pools in peat-based wetlands (mires).. Data from small datasets from Japan and Spain also fell within the range of the New Zealand data: thus the combination of higher pH and lower Ca may not be unique to the New Zealand / Tasmania region. Implications for diatom community composition (if any) remain to be determined, but given the wide and inconsistent pH ranges in which *Eunophora* species were found in New Zealand and Tasmanian [II], it seems unlikely that the pH of overlying waters directly determines whether this genus thrives or not.

The two-year study also confirmed that, as estimated from landscape-scale data in the habitat-wide analysis [I], mire pools were oligotrophic for most of the year. Again, even in this localised area there were differences in nutrient levels between sites, though these were less marked than, and unrelated to, the major gradients in water chemistry. Nutrient gradients were independent of the Ca / pH gradient, which is consistent with patterns in Northern Europe.

3.3 Coexistence of endemic and cosmopolitan taxa [IV, V]

What are the characteristics of tarns/bogs that might select against competing cosmopolitan taxa and allow coexistence with endemic taxa?

The key concept considered in addressing this question was invasibility, defined as: "the susceptibility of an environment to colonisation and establishment by individuals from species not currently part of the resident community" (Davis et al. 2005). Over the past ten years or so a common theme in the ecological literature has been identification of properties of biological communities which make them susceptible to invasions. Discussion has largely centred on whether species-rich communities are more resistant to invasions than species-poor communities. Conflicting results have lead to the so-called "invasion paradox" (e.g., Sax and Brown 2000), which suggests that scale is involved. Thus, numerous experiments at small spatial scales have shown that high-diversity communities are less likely to be invaded (e.g., Naeem et al. 2000), leading to a negative relationship between diversity and invasibility. In contrast, at larger scales in natural communities, a more common finding is that more diverse communities tend to include more non-native species (e.g., Stohlgren et al. 1999), suggesting a positive relationship between diversity and invasibility. These analyses have taken the view that diversity drives invasibility. However, the opposite has recently been proposed. In other words, invasibility is an intrinsic, dynamic property of biological communities that drives diversity (Davis et al. 2005). Here I used this latter approach to assess invasibility.

In either approach, disturbance is generally accepted as the single most important process that increases invasibility (Elton 1958, Huston 1994, and numerous subsequent publications, see IV). Because diatom communities often comprise coexisting populations of both endemic and cosmopolitan taxa, these organisms provide a suitable model for investigating the differential effects of disturbances on species with widely differing range sizes. Intuitively it is expected that species with cosmopolitan distributions are better dispersers and colonisers than species with restricted range sizes (i.e. endemic species).

The habitat-wide analysis [I] indicated that a low level of physical disturbance – in other words, habitat stability – is associated with the maintenance of endemic diatom taxa in New Zealand, and that tarns and mire pools dominate low productivity habitats in this category. A testable hypothesis arising from this was that, at a local scale, endemic diatom species should be more sensitive than

coexisting cosmopolitan species to physical disturbances. At the same time, responses to disturbances would be expected to vary according to the intrinsic invasibility of the environment, with stronger responses at the least invasible sites. I tested these hypotheses in a series of field observations and experiments at Bealey [IV].

First, I assessed the response of benthic diatom communities at four sites to natural physical disturbances. Observations at the sites over two years, including scrutiny of many benthic samples, indicated that the only significant source of physical disturbance in the study area was wind-induced wave perturbations. There was no evidence of regular medium-scale biotic disturbances (e.g., invertebrate or amphibian grazing). Occasional larger-scale disturbances by birds were usually localised in small areas. Wind-induced substrate disturbance was estimated to occur at two of the four study sites. One site was unaffected because of small size, and the second because of highly consolidated substrate.

Data from two summer seasons showed a significant negative correlation at one site only between wind speed and both the absolute abundance and proportion of endemic diatom biovolumes. Cosmopolitan diatom abundances were unrelated to wind speed, as were abundances of both groups of diatom taxa at all other sites. Because densities of endemic diatoms were already high at this one site, the overall effect on endemic diatom biovolumes was small, and possibly probably biologically insignificant in the long term.

In a second experiment, I investigated the effect of small-scale artificial disturbances at four sites over two months in the growing season. The disturbances were more severe than would be expected from wind disturbance in that the substrate was thoroughly mixed, but they were very small (scale of centimetres) such that fast recovery would be expected in taxa capable of rapid colonisation and growth.

Following the disturbances, I recorded significant declines in endemic diatom biovolume at the two sites with the largest initial populations of endemics. Conversely, biovolumes of non-endemic taxa were unchanged at all three sites. At the most severely affected site, diversity of non-endemic taxa (as species richness and the Shannon diversity index) also increased significantly following disturbance. Thus, at this site not only did disturbance have a negative impact on the endemic diatom group, but it was associated with recolonisation by additional non-endemic taxa. It should be noted that a single large-sized species, *Eunophora* cf. *oberonica*, was responsible for much of the endemic species responses (by biovolume), and this was very likely due to specialised habitat requirements by this species (see below). Nevertheless, a small species, *Kobayasiella* sp. A responded similarly at the same sites.

As hypothesised, differential responses among the sites were could be explained by differences in initial invasibility, assessed using the model proposed by Davis et al. (2005) (see above). In this approach, in addition to disturbances, the intrinsic invasibility of a site is determined by resource availability, which itself depends on prior colonisation from a regional species pool. If resident

species have already sequestered available resources, then it is unlikely that further species can successfully colonise. However, if there are surplus resources, then it follows that new colonising species may be able to persist. Although invasibility cannot be measured easily, it appears feasible to *rank* the property at neighbouring sites. To do this I first ranked resource availability by comparing dissolved water column P (likely to be limiting in these environments – see III) and dissolved Si, and then resource use by comparing benthic chlorophyll *a*. My rankings showed that the two sites with largest proportions of endemic species and lowest diversity were least invasible.

It was also clear that the gradient of invasibility was paralleled by a gradient of consolidation of the organic substrate in each pool: the firmest, most consolidated substrates were less invasible than loose unconsolidated material. This was interpreted as representing a gradient of increasing connection between the substrate and the overlying water column [also see V]. In all pools, the substrate was dominated by Cyanobacteria and to varying degrees resembled the stratified microbial mats described from other locations (e.g., Vincent et al. 1993). The interstitial water in very cohesive mats typically has very much higher nutrient and dissolved ion concentrations than the overlying water (Villeneuve et al. 2001), which could provide specialised habitat for resident algae.

The result of the small-scale disturbance experiment was reinforced by an unreplicated, "natural experiment" at the site most severely affected by the small-scale disturbance. During the first year of sampling, a substantial part of the sampling area at this site was disturbed by Canada geese, which apparently do not normally frequent the Bealey tarn area (Department of Conservation, Arthur's Pass, pers. comm.). The disturbed area was subsequently sampled at intervals over the next two years along with controls from adjacent undisturbed areas.

Both the proportion and absolute biovolume of endemic diatom taxa declined markedly following the goose disturbance. Even after two years, no clear recovery was evident. On the other hand, non-endemic biovolumes were unaffected by the disturbance and showed signs of increasing (compared to those in the control samples) towards the end of the sampling period, indicating increased invasibility of the disturbed area. A further indication of this was that species that had not previously been recorded at this site started to appear in the samples. All were non-endemic.

There were inconsistent responses in the species originally present. In particular, again, *Eunophora* cf. *oberonica* was responsible for much of the collective decline of endemic taxa. Another smaller assumed endemic species, *Kobayasiella* sp., initially declined in response to the disturbance, but recovered within a year. A third assumed endemic species, *Frustulia* sp. A, responded positively following the disturbance and retained elevated populations compared to those in control samples until the end of the sampling period.

Species-specific responses may result from a range of factors, including environmental requirements, the presence or absence of motility, differences in growth rates and likely evolutionary history. For example, it is generally accepted that small diatom species have faster

division rates than larger species (Baars 1983, Mizuno 1991). Also, species showing motility would be expected to recolonise from adjacent undisturbed areas faster than non-motile species. Motile species could also move upwards through the disturbed substratum to a favourable position. Together these factors would explain the response discrepancy between *Kobayasiella* sp. (a very small, motile species) and *Eunophora oberonica* (a relatively large diatom[4] in which motility has not been observed, personal observation). The most important driver of the sensitivity of *Eunophora* cf. *oberonica* to disturbances (in both the small-scale experiment and the larger goose disturbance) is likely to have been destruction of a specific micro-habitat (as discussed above) within the interstices of the relatively firm cyanobacterial mats which formed the substrate of the pools in which this species was common.

The significance of physical stability in the maintenance of at least some distinctive endemic diatom taxa was thus confirmed by these experiments [IV]. However, it was notable that especially in the two more invasible sites, several endemic diatom species were apparently unaffected by the experimental disturbances (e.g. *Amphora* (*Eunophora*) *berggrenii*, *Stenopterobia* sp. A, *Kobayasiella* sp. A, and *Encyonopsis* sp. A), suggesting no real difference between the two groups of species at these sites. (See also the comment above about *Frustulia* sp. A). Just one non-endemic species (*Frustulia saxonica* – a relatively large species) was adversely affected by the disturbances.

Having established the importance of disturbances and environmental invasibility in driving levels of endemism in some mire pool habitats, I then considered alternative theories of species coexistence. The overarching question was: what are the relative roles of processes such as traditional niche partitioning (spatial and temporal) (e.g., Wright 2002) and its more recent analogy, environmental variability (Davies et al. 2004, Tilman 2004); neutral dispersal (e.g., Hubbell's model, see McGill 2003b); and the effects of different dispersal abilities (e.g., the "spatial storage effect", Chesson 2000) in shaping the coexistence patterns we see in benthic diatoms? The question has already been considered in a review relating to diatoms, in which it was concluded that metapopulation dynamics (neutral dispersal) was important, but that the whole range of alternative processes also contributed (Soininen, 2006).

In this analysis I investigated whether coexisting endemic and non-endemic diatom species differed in their abundance patterns, and compared these patterns to those described for larger organisms. I focussed on species abundance–occupancy and abundance– persistence relationships, which are typically positive for most organism groups, the former being "… one of the most general patterns in ecology" (Gaston et al. 2000). The pattern is that species that are widely distributed also tend to be more abundant than species that have narrow, restricted distributions. Multiple mechanisms have been proposed to explain this pattern (see Gaston et al. 2000 for a detailed discussion; also see V). The less commonly studied abundance–persistence relationship is

[4] The biovolume of *Eunophora oberonica* is estimated to be at least about 40 times that of *Kobayasiella* sp.

similar: species that are abundant tend to be present in community for a greater proportion of the time than rare species (Magurran 2007). Abundance–persistence is also linked to the core and satellite species hypothesis, which maintains that species in a community can be separated into populations with differing properties according to their abundance and occupancy / persistence (Hanski 1982).

To investigate these patterns in diatoms, I used data gathered at three different scales: (1) from mire pools throughout the South Island (a subset of the data from I); (2) from multiple pools at Bealey (the dataset from II); (3) temporal data over two years from four pools at Bealey. For each dataset I examined the species abundance–occupancy (or persistence) relationship and compared the patterns for endemic and non-endemic species. My expectation was that any departures from the positive relationships seen in larger organisms should be evident only at the single site scale. Magurran (2007) stressed that temporal abundance–persistence relationships typically reflect abundance–occupancy patterns and can assist understanding of coexistence mechanisms in rare species. I therefore examined the temporal data more closely, and with reference to environmental data available for each of the pools.

All the abundance–occupancy relationships were positive, as expected, and consistent with patterns found for benthic stream diatoms (Soininen and Heino 2005). There was no difference between the relationships for endemic and non-endemic diatoms in the Bealey dataset. It was not possible to statistically test the South Island dataset because of the wide spread of the data, but the patterns were visually similar. Further, in both cases, endemic species covered the entire range of abundances, suggesting that the patterns were regionally driven, rather than from a global species pool. There was no relationship between endemic and non-endemic species richness in either the South Island or Bealey datasets, in contrast to positive relationships seen in larger organisms (e.g., Fattorini 2007). A positive endemic – non-endemic relationship is analogous to the positive native – non-native species richness relationships reported at large scales (e.g., Stohlgren 1999). Its apparent absence in the present diatom datasets is therefore interesting and indicates that even in habitats most favourable for maintenance of endemism in diatoms [I], non-endemics have higher diversity than expected. A likely explanation is that the non-endemics have been part of the community for a very long time (Foissner 2006).

Abundance–persistence relationships were also positive, but endemic and non-endemic species showed site-specific differences. Again the gradient reflected that of assessed invasibility of the four pools [IV]. The relationships were indistinguishable at the two most invasible sites, but diverged at the least invasible sites, which also had lowest species diversity and highest endemism. Responses to abiotic variables were consistent with this pattern (i.e., more significant responses at the most invasible sites), confirming my earlier conclusion [IV] that invasibility was linked to the gradient of connectivity between the substrate and overlying water (see above, p. 198). In addition, I found that diversity of endemic species was lower than that of non-endemics at all four sites, and

at the two most invasible sites non-endemic diversity showed a clear seasonal signal. Differences in temporal variability between endemics and non-endemics are explained as follows (see Glazier 1986). An endemic species will persist if it is capable of fully exploiting a suitable habitat, such that the community resists invasions, *and* if it can maintain dominance through seasonal perturbations. Species with narrow ranges that fail to meet these conditions will tend towards extinction. On the other hand, widespread cosmopolitan taxa will remain widespread despite responding to seasonal perturbations and interspecific competition because they are, in general, good dispersers and colonisers. If a local population becomes depleted, there will always be a source of new propagules ready to recolonise.

In this study [V], I concluded that on regional (South Island) and local (Bealey) scales endemic and non-endemic diatom species in mire pools follow patterns consistent with those of larger organisms, except that there are more non-endemics than expected. This suggests that the non-endemic species are historical components of the communities. At the single locality scale, some endemic species, such as *Eunophora* cf. *oberonica*, appear to have specialized habitat requirements that allow them to dominate in essentially non-invasible environments.

3.4 Conclusions

Although New Zealand's freshwater benthic diatom flora largely comprises cosmopolitan taxa, I have found that there is a larger element of endemism than has been assumed to date, where "endemic" is defined as occurring only in a bioregion encompassing New Zealand, Tasmania and Eastern Australia. Despite the general assumption of ubiquity in microorganisms, the distributions of these endemic taxa in New Zealand largely conform to patterns observed in higher plants. This is interpreted as evidence that the endemic component comprises species whose range sizes are constrained by dispersal potential.

Tarns and mire pools in subalpine areas are shown to support unusually high proportions of endemism (in terms of the total biovolume of diatom individuals in a community), as a result of the generally low disturbance and low productivity in these environments. It is possible that mire pools in New Zealand have unique environmental characteristics (e.g., unusually high pH at low Ca concentrations compared to similar European systems), and this may account for their unusual complement of species. These characteristics appear to be shared by mire pools in Tasmania. However, there are reports of similar conditions in localised areas in the Northern Hemisphere, so the environment is apparently not unique with respect to pH and Ca.

On a broad scale, abundance–occupancy patterns of benthic diatoms in mire pools in New Zealand (including endemic and non-endemic groups separately) are consistent with those for larger organisms, and for stream diatoms. It appears, however, that despite there being more endemism than traditionally assumed, numbers of endemic taxa are low compared to non-endemics. A likely explanation is the great length of time available for these small species to

disperse. At the scale of individual localities, communities dominated by endemic species were less invasible (as assessed using measures of resource availability and resource use) than those with higher proportions of non-endemic species. Unfortunately, because the two least invasible sites (of four sites studied) were dominated in terms of biovolume by a single endemic taxon (*Eunophora* cf. *oberonica*), with one other endemic taxon (*Kobayasiella* sp. A) also very common, it is difficult to draw general conclusions about the responses of endemic taxa. However, both these species thrive in very stable environments, and when this natural stability was disrupted, both were adversely affected. *Eunophora* cf. *oberonica*, in particular, appears to possess highly specialised habitat requirements and therefore is especially vulnerable to the effects of habitat destruction. Other endemic taxa that can persist in naturally more invasible communities apparently respond in the same way as most of the non-endemic taxa in those environments.

3.5 Further questions

This work has raised many questions, some of which could be partly addressed using existing data, but most of which would require further study.

The habitat requirements of *Eunophora* could be investigated further. What are the precise conditions within the cyanobacterial mat that favour proliferation of this species? What are the limits to survival of *Eunophora* cf. *oberonica* compared to those of *Amphora* (*Eunophora) berggrenii*? Are there facilitative relationships with the cyanobacteria that form the structure of the mats? What are the processes that maintain the structure of the microbial mats, and would disruption of those processes threaten *Eunophora* species? One possibility considered is that a positive feedback process operates, which both requires, and helps to retain, the relatively high water clarity noted in the pool with the most developed cohesive microbial mats (see paper III and IV). The hypothesis is that the cohesive cyanobacterial community may be maintained by continual exposure to UVB radiation through the clear water (e.g., Sheridan 2001), and at the same time the firm mat surface limits wind resuspension both of dissolved nutrients and of organic substrate by-products that might colour the water. This is speculative, but could be tested experimentally. I also speculate that higher summer UVB levels in New Zealand compared to those in the Northern Hemisphere (McKenzie at al. 1999) may enhance rates of both DOC photodegradation and cohesive mat development. Further, climate change (in particular temperature increases) are leading to increased release of DOC into surface waters (e.g., Pastor et al. 2003). Could such changes impact maintenance of microbial mats (and their associated diatom communities) in New Zealand's subalpine environments? Further, would accompanying declines (or increases) in rainfall exacerbate these changes?

The definition of endemic and non-endemic species clearly requires more investigation. Is the morphological approach used throughout this study sufficient, or is a more integrated approach

necessary (e.g., morphology, ecology, reproductive biology, molecular structure)? Further studies such as that by Vanormelingen et al. (2007) would be relevant here.

On the biogeographical front, a more thorough investigation of the congruence of diatom communities between Tasmania and New Zealand (see Vanhoutte et al. 2006b) could throw light on some more fundamental biogeographical questions in this region (e.g., relating to dispersal vs. vicariance). Also how frequently are new diatom species arriving in New Zealand, and how much is this changing / has this changed the "native" communities. The recent arrival of *Didymosphenia geminata* in the South Island, almost certainly by anthropogenic means, highlights the fact that other non-endemic species may have arrived via non-natural dispersal (Kociolek and Spaulding 2000). Palaeoecological studies may also help to address this question.

4. References

Agard, J.; Hubbard, R.; Griffith, J.K. (1996). The relation between productivity, disturbance and the biodiversity of Caribbean phytoplankton: applicability of Huston's dynamic equilibrium model. Journal of Experimental Marine Biology and Ecology 202: 1-17.

Agnew, A.D.Q.; Rapson, G.L.; Sykes, M.T.; Bastow Wilson, J. (1993). The functional ecology of *Empodsima minus* (Hook f.) Johnson & Cutler in New Zealand ombrotrophic mires. – New Phytol. 124: 703-710.

Anonymous (1975). Proposals for a standardization of diatom terminology and diagnoses. Nova Hedwigia, Beih. 53: 323-354.

Anonymous (2000). The New Zealand biodiversity strategy. Department of Conservation and Ministry for the Environment, Wellington. (http://www.biodiversity.govt.nz/pdfs/-picture/nzbs-whole.pdf)

APHA (1998). Standard Methods for the Analysis of Water and Wastewater. 20th Edition. American Public Health Association, Washington DC

Arvola, L.; Metsala, T-R.; Simila, A.; Rask, M. (1990). Seasonal fluctuations in the chemistry of small forest lakes in southern Finland with special reference to acidity. Aqua Fennica 20: 71-9.

Azovsky, A. (2002). Size-dependent species-area relationships in benthos: is the world more diverse for microbes? Ecography 25: 273-282.

Baars, J. W. M. (1983). Autecological investigations on freshwater diatoms 1. Archiv für Hydrobiologie Supplement 67,1 (Algological Studies 34): 11 - 18.

Baas-Becking, L.G.M. (1934). Geobiologie of inleiding tot de milieukunde. The Hague, Van Stockum and Zoom.

Baines, S.B.; Webster, K.E.; Kratz, T.K.; Carpenter, S.R.; Magnuson, J.J. (2000). Synchronous behaviour of temperature, calcium, and chlorophyll in lakes of northern Wisconsin. Ecology 81: 815-825.

Barber, H. (1962). Freshwater diatoms from Cass, South Island, New Zealand. Journal of the Quekett Microscopical Club, Series 4, 29: 17–20.

Battarbee, R.W.; Charles, D.F.; Dixit, S.S.; Renberg, I. (1999). Diatoms as indicators of surface water acidity. Pp. 85-127 in: Stoermer, E.F.; Smol, J.P. (eds). The Diatoms: Applications for Environmental and Earth Sciences. Cambridge University Press, New York.

Battarbee, R.W.; Flower, R.J.; Juggins, S.; Patrick, S.T.; Stevenson, A.C. (1997). The relationship between diatoms and surface water quality in the Høylandet area of Nord-Trøndelag, Norway. Hydrobiologia 348: 69-80.

Behnke, A.; Friedl, T.; Chepurnov, V.A.; Mann, D.G. (2004). Reproductive compatibility and rDNA sequence analyses in the *Sellaphora pupula* species complex (Bacillariophyta). Journal of Phycology 40: 193-208.

Beier, T.; Lange-Bertalot, H. (2007). A synopsis of cosmopolitan, rare and new *Frustulia* species (Bacillariophyceae) from ombrotrophic peat bogs and minerotrophic swamps in New Zealand. Nova Hedwigia 85: 73-91.

Bell, T.; Ager, D.; Song, J.I.; Newman, J.A.; Thompson, I.P.; Lilley, A.K.; Van Der Gast, C.J. (2005). Larger islands house more bacterial taxa. Science 308: 1884.

Bennion, H. (1995). Surface-sediment diatom assemblages in shallow, artificial, enriched ponds and implications for reconstructing trophic status. Diatom Research 10: 1-19.

Beszteri, B.; Ács, É.; Medlin, L.K. (2005). Ribosomal DNA sequence variation among sympatric strains of the *Cyclotella meneghiniana* complex (Bacillariophyceae) reveals cryptic diversity. Protist 156: 317-333.

Biggs, B.J.F. (1995). The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. Freshwater Biology 33: 419–438.

Biggs, B.J.F.; Kilroy, C. (2000). Stream periphyton monitoring manual. Published by NIWA for the New Zealand Ministry for the Environment. 226 p. (available online at www.niwa.co.nz/ncwr/tools/periphyton/).

Biggs, B.J.F.; Kilroy, C.; Lowe, R.L. (1998b). Periphyton development in three valley segments of a New Zealand grassland river: test of a habitat matrix conceptual model within a catchment. Archiv für Hydrobiologie 143(2): 147 - 177.

Biggs, B.J.F.; Smith, R.A. (2002). Taxonomic richness of stream benthic algae: effects of flood disturbance and nutrients. Limnology and Oceanography 47: 1175–1186.

Biggs, B.J.F.; Stevenson, R.J.; Lowe, R.L. (1998a). A habitat matrix conceptual model for stream periphyton. Archiv für Hydrobiologie 143: 21–56.

Birks, H.J.B.; Line, J.M.; Juggins, S.; Stevenson, A.C.; ter Braak, C.J.F. (1990). Diatoms and pH reconstruction. Philosophical Transactions of the Royal Society, London Series B, Biological Sciences 327: 263-278.

Blackburn, T.; Lawton, J.; Perry, J.N. (1992). A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. Oikos 65: 107–112.

Blumenshine, S.; Vadeboncoeur, Y.; Lodge, D.M.; Cottingham, K.L.; Knight, S.E. (1997). Benthic-pelagic links: responses of benthos to water-column nutrient enrichment. Journal of the North American Benthological Society 16: 466-479.

Bonnett, S.A.F.; Ostle, N.; Freeman, C. (2006). Seasonal variations in decomposition processes in a valley-bottom riparian peatland. Science of the Total Environment 370: 561-573.

Bragazza, L. (1994). Seasonal changes in water chemistry in a bog on the Southern Alps. Suo 44: 87-92.

Bragazza, L.; Gerdol, R. (2002). Are nutrient availability and acidity-alkalinity gradients related in Sphagnum-dominated peatlands? Journal of Vegetation Science 13: 473-482.

Bragg, O.M. (2002). Hydrology of peat-forming wetlands in Scotland. Science of the Total Environment 294: 111-129.

Bragg, O.M.; Tallis, J.H. (2001). The sensitivity of peat-covered upland landscapes. Catena 42: 345-360.

Brassac, N.M.; Torgan, L.C.; Ludwig, T.A.V. (2003). Transfer of *Surirella schweickerdtii* to the genus *Stenopterobia*. Diatom Research 18: 185-190.

Burke, M.J.W.; Grime, J. P. (1996). An experimental study of plant community invasibility. Ecology 77: 796–790.

Burns, C.W. (1991). New Zealand lakes research, 1967-91. New Zealand Journal of Marine and Freshwater Research 25: 359-379.

Burns, C.W.; Butler, M.I.; Cuttance, P.M. (1984). Invertebrates, macroalgae, and chemical features in morainic ponds near Lakes Tekapo and Ohau, including new distribution records of Crustacea. New Zealand Journal of Marine and Freshwater Research 18: 197 - 210.

Burrows, C.J. (1972). Mires of the Manapouri – Te Anau lowlands. Proceedings of the New Zealand Ecological Society 19: 75-99.

Camburn, K. E.; Charles, D. F. (2000). Diatoms of low-alkalinity lakes in the Northeastern United States. Academy of Natural Sciences of Philadelphia Special Publication 18.

Campbell, D.I.; Williamson, J.L. (1997). Evaporation from a raised peat bog. Journal of Hydrology 193: 142-160.

Campbell, E.O. (1983). Mires of Australasia. Pp. 153-180 in: Gore, A.J.P. (ed.). Mires: swamp, bog, fen and moor. Ecosystems of the world 4B. Elsevier, Amsterdam.

Carlson, R. (1977). A trophic state index for lakes. Limnology and Oceanography 22: 361-369.

Carrick, H.J.; Lowe, R.L. (1988). Response of Lake Michigan algae to in situ enrichment with Si, N and P. Canadian Journal of Fisheries and Aquatic Sciences 45: 271-279.

Carter, J. R.; Bailey-Watts, A. (1981). A taxonomic study of diatoms from standing freshwaters in Shetland. Nova Hedwigia 33: 513–628.

Carter, J. R.; Denny, P. (1987). Freshwater algae of Sierra Leone IV. Bacillariophyceae: Part (ii) diatoms from the coastal region of the southern province. Nova Hedwigia 44: 229–275.

Cassie, V. (1983). A history of freshwater diatom research in New Zealand. Archives of Natural History 11: 223-231.

Cassie, V. (1984). Checklist of the Freshwater Diatoms of New Zealand. Bibliotheca Diatomologica 4: 1-129.

Cassie, V. (1989). A contribution to the study of New Zealand diatoms. Bibliotheca Diatomologica 17: 51–266.

Cassie-Cooper, V. (1994). Freshwater algal research in New Zealand: an update. Archives of Natural History 21: 113-130.

Charles, D. (1986). A new diatom species, *Fragilaria acidobiontica*, from acidic lakes in northeastern North America. Pp. 35–44 in: Smol, J.; Battarbee, R.; Davis, R.; Merilainene, J. (eds). Developments in Hydrobiology. Diatoms and lake acidity. Dordrecht, Dr W Junk..

Chave, J. (2004). Neutral theory and community ecology. Ecology Letters 7: 241-253.

Chen, G.-F.; Wang, G.-C.; Zhang, B-Y.; Fan, X-L (2007). Morphological and phylogenetic analysis of *Skeletonema costatum*-like diatoms (Bacillariophyta) from the China Sea. European Journal of Phycology 42: 163-175.

Chepurnov, V.A.; Mann, D.G.; Sabbe, K.; Vyverman, W. (2004). Experimental studies on sexual reproduction in diatoms. International Review of Cytology 237: 91-153.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31: 343-366.

Clarke, K. R.; Warwick, R. M. (2001). Change in marine communities. An approach to statistical analysis and interpretation. 2nd edition. Plymouth Marine Laboratory, UK.

Clarke, K.R.; Ainsworth, M. (1993). A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92: 205-219

Clarkson, B.R.; Schipper, L.A.; Clarkson, B.D. (2004). Vegetation and peat characteristics of restiad bogs on Chatham Island (Rekohu), New Zealand. New Zealand Journal of Botany, 42: 293-312.

Cleve, P.T. (1881). On some new and little known diatoms. Kongliga Svenska Vetenskaps-Akademiens Handlingar, 18. 5: 3-6.

Cleve-Euler, A. (1953). Die Diatomeen von Schweden und Finnland. Part 2. K. Kongliga Svenska Vetenskaps-Akademiens Handlingar, 4. 1: 1–158.

Close, M.E.; Davies-Colley, R.J. (1990). Baseflow water chemistry in New Zealand rivers. 1. Characterisation. New Zealand Journal of Marine and Freshwater Research 24: 343-356.

Clymo, R.S. (1987). Interactions of *Sphagnum* with water and air. Pp. 513-529 in: Hutchinson, T.C.; Meema, K.M. (eds). Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Systems. Springer-Verlag, Berlin, Heidelberg.

Cochran, U.A. (2002). Detection of large Holocene earthquakes in the sedimentary record of Wellington, New Zealand, using diatom analysis. Unpublished PhD Thesis, Victoria University, Wellington.

Cohn, S. A.; Weitzell, R.E. (1996). Ecological considerations of Diatom cell motility. I. Characterization of motility and adhesion in four diatom species. Journal of Phycology 32: 928 - 939.

Cook, L.G.; Crisp, M.D. (2005). Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. Journal of Biogeography 32: 741– 754.

Cox, E. (1994). Morphological variation in widely distributed diatom taxa: taxonomic and ecological implications. 13th International Diatom Symposium.

Cox, E. J. (1987). *Placoneis* Mereschkowsky: the re-evaluation of a diatom genus originally characterized by its chloroplast type. Diatom Research 2: 145-157.

Cox, E.J. (1979). Taxonomic studies on the diatom genus *Navicula* Bory. The typification of the genus. Bacillaria 2: 137-153.

Cox, E.J. (1999). Studies on the diatom genus *Navicula* Bory. VIII. Variation in valve morphology in relation to the generic diagnosis based on *Navicula tripunctata* (O.F. Müller) Bory. Diatom Research 14: 207-237.

Créach, V.; Ernst, A.; Sabbe, K.; Vanelslander, B.; Vyverman, W.; Stal, L.J. (2006). Using quantitative PCR to determine the distribution of a semicryptic benthic diatom, *Navicula phyllepta* (Bacillariophyceae). Journal of Phycology 42: 1142-1154.

Croasdale, H.; Flint, E.A. (1986). Flora of New Zealand : freshwater algae, Chlorophyta, desmids : with ecological comments on their habitats. Volume I. Wellington : Govt. Print.

Croasdale, H.; Flint, E.A. (1988). Flora of New Zealand : freshwater algae, Chlorophyta, desmids : with ecological comments on their habitats. Volume II. Wellington : Govt. Print.

Croasdale, H.; Flint, E.A.; Racine, M.M. (1994). Flora of New Zealand. Freshwater algae, Chlorophyta, desmids, with ecological comments on their habitats. Volume III. Manaaki Whenua Press, Lincoln, Canterbury, New Zealand.

Davies, K.E.; Chesson, P.; Harrison, S.; Inouye, B.D.; Melbourbe, B.A.; Rice, K.J. (2005). Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology 86: 1062-1610.

Davies, S.J., Metcalfe, S.E.; Callabero, M.E.; Juggins, S. (2002). Developing diatom-based transfer functions for Central Mexican lakes. Hydrobiologia 467: 199-213.

Davies-Colley, R.J.; Vant, W.N.; Smith, D.G. (1993). Colour and clarity of natural waters. Science and management of optical water quality. Ellis Horwood, Chichester.

Davis, M.A. (2003). Biotic globalization: does competition from introduced species threaten biodiversity? BioScience 53: 481-489.

Davis, M.A.; Grime, P.J.; Thompson, K. (2000). Fluctuating resources in plant communities, a general theory of invasibility. Journal of Ecology 88: 528–534.

Davis, M.A.; Thompson, K.; Grime, J.P. (2001). Charles S. Elton and the dissociation of invasion ecology with the rest of ecology. Diversity and Distributions 7: 97-102.

Davis, M.A.; Thompson, K.; Grime, J.P. (2005). Invasibility: the local mechanism driving community assembly and species diversity. Ecography 28: 696–704.

Dickinson, K.J.M.; Chague-Goff, C.; Mark, A.F.; Cullen, L. (2002). Ecological processes and trophic status of two low-alpine patterned mires, south-central South Island, New Zealand. Australian Ecology 27: 369 - 384.

Dodds, W.; Priscu, J. (1990). A comparison of methods for assessment of nutrient deficiency of phytoplankton in a large oligotrophic lake. Canadian Journal of Fisheries and Aquatic Sciences 47: 2328-2338.

Dolan, J. (2005). An introduction to the biogeography of aquatic microbes. Aquatic Microbial Ecology 41: 39-48.

Douglas, M.S.V.; Smol, J.P. (1995). Periphytic diatom assemblages from high Arctic ponds. Journal of Phycology 31: 60 - 69.

Downes, M. (1988) Methods manual. Taupo Research Laboratory Report, DSIR, Taupo. 70 p.

Downes, M. (2001). NIWA Christchurch auto-analyser methods. NIWA Internal Report No. 103. NIWA, Christchurch, New Zealand.

Droop, S. J.M.; Mann, D.G.; Lokhorst, G.M. (2001). Spatial and temporal stability of demes in *Diploneis smithii*/*D. fusca* (Bacillariophyta) supports a narrow species concept. Phycologia 39: 527 - 546.

Edlund, M.B.; Stoermer, E.F. (1997). Ecological, evolutionary and systematic significance of diatom life histories. Journal of Phycology 33: 897 - 918.

Elton, C.S. (1958). The Ecology of Invasions by Animals and Plants. Methuen, London.

Fallu, M.-A., Allaire, N.; Pienitz, R. (2000). Freshwater diatoms from northern Québec and Labrador (Canada). Species–environment relationships in lakes of boreal forest, forest-tundra and tundra regions. Bibliotheca Diatomologica 45: 1-200.

Fattorini, S. (2007). Levels of endemism as are not necessarily biased by the co-presence of species with different range sizes: a case study of Vilenkin and Chikatunov's models. Journal of Biogeography 34: 994-1007.

Fenchel, T. (2005). Cosmopolitan microbes and their 'cryptic' species. Aquatic Microbial Ecology 41: 49-54.

Fenchel, T.; Finlay, B.J. (2004). The ubiquity of small species: patterns of local and global diversity. BioScience 54: 777-784.

Fenchel, T.; Finlay, B.J. (2006). The diversity of microbes: resurgence of the phenotype. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 361: 1965-1973.

Finlay, B.J. (2002). Global dispersal of free-living microbial eukaryote species. Science 296: 1061 - 1063.

Finlay, B.J.; Clarke, K. (1999). Ubiquitous dispersal of microbial species. Nature 400: 828.

Finlay, B.J.; Esteban, G.; Fenchel, T. (2004). Protist diversity is different? Protist 155: 15-22.

Finlay, B.J.; Maberly, S.C.; Cooper, J.I. (1997). Microbial diversity and ecosystem function. Oikos 80: 209-213.

Finlay, B.J.; Monaghan, E.; Maberly, S.C. (2002). Hypothesis: the rate and scale of dispersal of freshwater diatom species is a function of their global abundance. Protist 153: 261-273.

Flint, E.A. (1996). Some additions to the desmid flora of New Zealand. New Zealand Journal of Botany 34: 547-551.

Flint, E.A.; Williamson, D.B. (1999). Desmids (Chlorophyta) in a small tarn in central Canterbury. New Zealand Journal of Botany 37: 541-551.

Flower, R. (2005). A taxonomic and ecological study of diatoms from freshwater habitats in the Falkland Islands, South Atlantic. Diatom Research 20: 23-96.

Foged, N. (1978). Diatoms in Eastern Australia. Bibliotheca Phycologica 41: 1–243.

Foged, N. (1979). Diatoms in New Zealand, the North Island. Bibliotheca Phycologica 47: 1-225.

Foissner, W. (2006). Biogeography and dispersal of micro-organisms: a review emphasizing protists. Acta Protozoologica 45: 111-136.

Foster, D.; Fritz, S.C. (1987). Mire development, pool formation and landscape processes on patterned fens in Dalarna, Central Sweden. Journal of Ecology 75: 409-437.

Foster, D.R.; Wright, H.E. (1990). Role of ecosystem development and climate change in bog formation in central Sweden. Ecology 71: 450-463.

Fridley, J.D.; Brown, R.L.; Bruno, J.F. (2004). Null models of exotic invasion and scale-dependent patterns of exotic and native species richness. Ecology 85: 3215-3222.

Fridley, J.D.; Stachowicz, J.; Naeem, S.; Sax, D.F.; Seabloom, E.W.; Smith, M.D.; Stohlgren, T.J.; Tilman, D.; Von Holle, B (2007). The invasion paradox: reconciling pattern and process in species invasions. Ecology 88: 3-17.

Fritts, T.; Rodda, G. (1998). The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annual Review of Ecology and Systematics 29: 113-140.

Fritz, S.C., Cumming, B.F.; Gasse, F.; Laird, K.R. (1999). Diatoms and indicators of hydrologic and climatic change in saline lakes. Pp. 41-72 in Stoermer, E.F. and Smol, J. (eds). The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press.

Gaiser, E.; Johansen, J. (2000). Freshwater diatoms from Carolina Bays and other isolated wetlands on the Atlantic Coastal plain of South Carolina, USA, with descriptions of seven taxa new to science. Diatom Research 15: 75-130.

Gasse, F. (1978). Les diatomées holocènes d'une tourbière (4040 m) du montagne éthiopienne: le Mont Badda. Revue Algologie, N.S., 13: 105–149.

Gasse, F. (1986). East African diatoms. Taxonomy, ecological distributions. Bibliotheca Diatomologica 11: 1–195.

Gaston, K.J. (2003). The Structure and Dynamics of Geographic Ranges. Oxford University Press, New York.

Gaston, K.J.; Blackburn, T.; Greenwood, J.J.D.; Gregory, R.D.; Quinn, R.M.; Lawton, J.H. (2000). Abundance-occupancy relationships. Journal of Applied Ecology 37, Suppl. 1: 39-59.

Gaston, K.J.; Spicer, J.I. (2004). Biodiversity: an introduction. Second edition. Blackwell Science Ltd.

George, D.G.; Talling, J.F.; Rigg, E. (2000). Factors influencing the temporal coherence of five lakes in the English Lake District. Freshwater Biology 43: 449-461.

Gilbert, B.; Lechowicz, M. (2005). Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology 86: 1848-1855.

Glaser, P.H., Wheeler, G.A., Gorham, E.; Wright, H.E. (1981). The patterned mires of the Red Lake Peatland, northern Minnesota. Journal of Ecology 69: 575-599.

Glazier, D. (1986). Temporal variability of abundance and the distribution distribution of species. Oikos: 309-314.

Glazier, D.; Eckert, S. (2002). Competitive ability, body size and geographical range size in small mammals. Journal of Biogeography 29: 81-92.

Goff, J.R.; Rouse, H.L.; Jones, S.L.; Hayward, B.W.; Cochran, U.; McLea, W.; Dickinson, W.W.; Morley, M.S. (2000). Evidence for earthquake and tsunami about 3100 – 3400 years ago, and other catastrophic saltwater inundations recorded in a coastal lagoon, New Zealand. Marine Geology 170: 231-249.

Goldsborough, L.G.; Brown, D.J. (1991). Periphyton production in a small dystrophic pond on the Canadian Precambrian shield. Verh. – Int. Ver. theor. Angew. Limnol. 24: 1497-1502.

Goldsborough, L.G.; Robinson, G. (1996). Patterns in Wetlands. Pp. 77-117 in Stevenson, R.J.; Bothwell, M.L.; Lowe, R.L. (eds). Algal Ecology: Freshwater benthic ecosystems. Academic Press, San Diego.

Gore, A.J.P. (1983). Mires: swamp, bog, fen and moor. Ecosystems of the world. 4A. Elsevier, Amsterdam.

Gorham, E.; Bayley, S.E.; Schindler, D.W. (1984). Ecological effects of acid deposition upon peatlands: a neglected field in “acid-rain” research. Canadian Journal of Fisheries and Aquatic Sciences 41: 1256-1268.

Gorham, E.; Janssens, J.A.; Wheeler, G.A.; Glaser, P.H. (1987). The natural and anthropogenic acidification of peatlands. Pp. 493-512 in: Hutchinson, T.C.; Meema, K.M. (eds). Effects of atmospheric pollutants on forests, wetlands and agricultural systems. Springer-Verlag, Berlin, Heidelberg.

Gottlieb, A.; Richards, J.; Gaiser, E. (2005). Effects of desiccation duration on the community structure and nutrient retention of short and long-hydroperiod Everglades periphyton mats. Aquatic Botany 2005.

Graham, L.E.; Wilcox, L.W. (2000). Algae. Prentice-Hall Inc., Upper Saddle River, NJ.

Grieve, I.C.; Gilvear, D.G.; Bryant, R.G. (1995). Hydrochemical and water source variations across a floodplain mire, Insh Marshes, Scotland. Hydrological Processes 9: 99-110.

Gunnarsson, U.; Rydin, H.; Sjörs, H. (2000). Diversity and pH changes after 50 years on the boreal mire Skattlosbergs Stormosse, Central Sweden. Journal of Vegetation Science 11: 277-286.

Gurevitch, J.; Padilla, D. (2004). Are invasive species a major cause of extinctions? Trends in Ecology and Evolution 19: 470-474.

Hall, R.; Smol, J.P. (1992). A weighted-averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Colombia (Canada) lakes. Freshwater Biology 27: 417-434.

Hamilton, P.B.; Jahn, R. (2005). Typification of *Navicula affinis* Ehrenberg: type for the name of the genus *Neidium* Pfitzer. Diatom Research 20: 281-294.

Hamilton, P.B.; Poulin, M.; Charles, D.F.; Angell, M. (1992). Americanarum Diatomarum Exsiccata: CANA, voucher slides from eight acidic lakes in northeastern North America. Diatom Research 7: 25–36.

Hanski, I. (1982). Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38: 210-221.

Harper, M.A.; Cassie-Cooper, V.; Chang, F.H. et al. (in press). Phylum Ochrophyta - brown and golden-brown algae, diatoms, silicoflagellates, and kin. In: Gordon, D.P. (ed.), The New

Zealand Inventory of Biodiversity. Volume 3, Kingdoms Bacteria, Protozoa, Chromista, Plantae, and Fungi. Canterbury University Press, Christchurch.

Hawes, I.; Smith, R. (1993). Effect of localised nutrient enrichment on the shallow epilithic periphyton of oligotrophic Lake Taupo, New Zealand. New Zealand Journal of Marine and Freshwater Research 27: 365-372.

Hawes, I.; Smith, R. (1994). Seasonal dynamics of epilithic periphyton in oligotrophic Lake Taupo, New Zealand. New Zealand Journal of Marine and Freshwater Research 28: 1-12.

Heath, J. (2006). Quantifying temporal variability in population abundances. Oikos 115: 573-581.

Herben, T.; Mandák, B.; Bímová, K.; Münzbergová, Z (2004). Invasibility and species richness of a community: a neutral model and a survey of published data. Ecology 85: 3223-3233.

Hillebrand, H.; Azovsky, A. (2001). Body size determines the strength of the latitudinal diversity gradient. Ecography 24(3): 251-256.

Hillebrand, H.; Watermann, F.; Karez, R.; Berninger, U.-G. (2001). Differences in species richness patterns between unicellular and multicellular organisms. Oecologia 126:114-124.

Hustedt, F. (1930). Die Kieselaglen Deutschlands, Österreichs und der Schweiz. Part II (Band 7). Rabenhorst's Krytpogamen Flora. 845 p.

Hustedt, F. (1930). Die Susswasser-flora Mitteleuropas. Heft 10. Bacillariophyta (Diatomeae). Verlag von Gustav Fischer, Jena.

Huston, M.A. (1994). Biological Diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Huston, M.A. (2004). Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Diversity and Distributions 10: 167-178.

Huston, M.A.; DeAngelis, D. (1994). Competition and coexistence: the effects of resource transport and supply rates. The American Naturalist 144: 954-977.

James, M.; Hawes, I.; Weatherhead, M. (2000). Removal of settled sediments and periphyton from macrophytes by grazing invertebrates in the littoral zone of a large oligotrophic lake. Freshwater Biology 44: 311-326.

Johnson, P.; Gerbeaux, P. (2004). Wetland types in New Zealand. Department of Conservation, Wellington.

Johnson, P.N. (1980). Lake Ohau tarns and kettles: botanical report. Unpublished Botany Division report. DSIR, Botany Division, Dunedin.

Johnson, P.N. (1984). Report on botany of some inland Marlborough and north Canterbury tarns and lakes. Unpublished Botany Division report. DSIR, Botany Division, Lincoln.

Juggins, S. (2003). C^2 User guide: software for ecological and palaeocological data analysis and visualization. University of Newcastle, Newcastle-upon-Tyne, UK. 69 pp.

Jüttner, I.; Cox, E.J.; Ormerod, S.J. (2000). New or poorly known diatoms from Himalayan streams. Diatom Research 15: 237-262.

Kammer, P.; Mohl, A. (2002). Factors controlling species richness in alpine plant communities: an assessment of the importance of stress and disturbance. Arctic, Antarctic and Alpine Research 34: 398–407.

Kilroy, C. (2004). A new alien diatom *Didymosphenia geminata* (Lyngbye) Schmidt: its biology, distribution, effects and potential risks for New Zealand fresh waters. –NIWA Client Report CHC2004-128. (www.biosecurity.govt.nz/files/pests-diseases/plants/didymo/niwa-perlim-didymo-report.pdf)

Kilroy, C. et al. (2005). Ecological studies on *Didymosphenia geminata*. NIWA Client Report CHC2005-128. For Biosecurity New Zealand. 77 p.

Kilroy, C., Biggs, B.J.F.; Vyverman, W. (2007). Rules for macroorganisms applied to microorganisms: patterns of endemism in benthic freshwater diatoms. Oikos 116: 550-564.

Kilroy, C., Sabbe, K.; Bergey, E. A.; Vyverman, W.; Lowe, R. (2003). New species of *Fragilariforma* (Bacillariophyceae) from New Zealand and Australia. New Zealand Journal of Botany 41: 535-554.

Kilroy, C.: Biggs, B.J.F.; Vyverman, W.; Broady, P.A. (2006). Benthic diatom communities in subalpine pools in New Zealand: relationships to environmental variables. Hydrobiologia 561: 95-110.

Kilroy, C.: Biggs, B.J.F.; Vyverman, W.; Broady, P.A. (in revision). Spatial and temporal variability in mire pool limnology. Fundamental and Applied Limnology.

Kilroy, C.; Lagerstedt, M.; Davey, A.; Robinson, K. (2006). Studies on the survivability of the invasive diatom *Didymosphenia geminata* under a range of environmental and chemical conditions. NIWA Client Report CHC2006-116. 109 p. (For Biosecurity New Zealand)

Kingston, J.; Sherwood, A.; Bengtsson, R. (2001). Morphology and taxonomy of several *Fragilariforma* taxa from Fennoscandia and North America. In: Economou-Amilli, A. ed. Proceedings of the 16th International Diatom Symposium, Athens, Greece. University of Athens, Greece. Pp. 73–88.

Kling, G.W.; Kipphut, G.W.; Miller, M.M.; O'Brien, W.J. (2000). Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. Freshwater Biology 43: 477-497.

Knoppen, J.D. (1975). A morphological and taxonomic consideration of *Tabellaria* (Bacillariophyceae) from the north-central United States. Journal of Phycology 11: 236-244.

Kobayasi, H.; Naguma, T. (1988). Examination of the type materials of *Navicula subtilissima* Cleve (Bacillariophyceae). The Botanical Magazine, Tokyo 101: 239-253.

Kociolek, J.P. (1998). Does each genus of diatoms have at least one unique feature? – a reply to Round. Diatom Research 11: 177-179.

Kociolek, J.P.; Kingston, J. (1999). Taxonomy, ultrastructure, and distribution of some gomphonemoid diatoms (Bacillariophyceae: Gomphonemataceae) from rivers in the United States. Canadian Journal of Botany 77: 686-705.

Kociolek, J.P.; Spaulding, S.A. (2000). Freshwater diatom biogeography. Nova Hedwigia 71: 223–241.

Kociolek, J.P.; Spaulding, S.A.; Sabbe, K.; Vyverman, W. (2004). New *Gomphonema* (Bacillariophyta) species from Tasmania. Phycologia 43: 427-444.

Kociolek, J.P.; Stoermer, E.F. (1988). Taxonomy, ultrastructure and distribution of *Gomphoneis herculeana*, *G. eriense* and closely related species (Naviculales: Gomphonemataceae). Proceedings of the Academy of Natural Sciences of Philadelphia 140: 24–97.

Kociolek, J.P.; Stoermer, E.F. (2001). Taxonomy and ecology: a marriage of necessity. Diatom Research 16: 433 - 442.

Kolar, C., Lodge, D. (2001). Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16: 199-204.

Kooistra, W.H.C.F.; Medlin, L.K. (1996). Evolution of the diatoms (Bacillariophyta) IV. A reconstruction of their age from small subunit rRNA coding regions and the fossil record. Molecular Phylogenetics and Evolution 6: 391-407.

Krammer, K. (1982). Valve morphology in the genus *Cymbella* C.A. Agardh. Volume XI in Helmcke, J.-G.; Krammer, K. (eds). Micromorphology of Diatom Valves. J. Cramer, Vaduz.

Krammer, K. (1989). Valve morphology and taxonomy in the genus *Stenopterobia* (Bacillariophyceae). British Phycological Journal 24: 237-243.

Krammer, K. (1992). *Pinnularia*, eine Monographie der europaischen Taxa. Biobliotheca Diatomologica 26: 1-353.

Krammer, K. (1997a). Die cymbelloiden Diatomeen. Teil 1. Allgemeines und *Encyonema* part. Bibliotheca Diatomologica 37: 1-382.

Krammer, K. (1997b). Die cymbelloiden Diatomeen. Teil 2. *Encyonema* part, *Encyonopsis* and *Cymbellopsis*. Bibliotheca Diatomologica 37: 1-469.

Krammer, K. (2000). Diatoms of Europe. Diatoms of the European inland waters and comparable habitats (ed. H. Lange-bertalot). Volume 1. The genus *Pinnularia*. A.R.G. Ganter Verlag K.G.

Krammer, K.; Lange-Bertalot, H. (1991–1997). Süsswasserflora von Mitteleuropa. 2 Bacillariophyceae. Teil 1 – 4. Fischer, Stuttgart.

Laing, T. E.; Smol, J.P. (2000). Factors influencing diatom distributions in circumpolar treeline lakes of northern Russia. Journal of Phycology 36: 1035 - 1048.

Lange, M. (2005). Ecological laws: what would they be and why would they matter? Oikos 110: 394-403.

Lange-Bertalot, H. (1988). Die Gattung *Tabellaria* unter besonderer Beruchsichtigung an *Tabellaria ventricosa* Kutzing (Bacillariophyceae). Nova Hedwigia 46: 413 – 31.

Lange-Bertalot, H. (1989). Können *Staurosirella*, *Punctastriata* und weitere Taxa sensu Williams & Round als Gattungen der Fragilariaceae kritischer Prüfungen standhalten? Nova Hedwigia 49: 79–106.

Lange-Bertalot, H. (1996). *Kobayasia bicuneus* gen. et sp. nov. Iconographica Diatomologica 4: 277-287.

Lange-Bertalot, H. (1999). *Kobayasiella* nom. nov. ein neuer Gattungsname fur *Kobayasia* Lange-Bertalot 1996. Iconographica Diatomologica 6: 272-275.

Lange-Bertalot, H. (2001). Diatoms of Europe. Diatoms of the European inland waters and comparable habitats (ed. H. Lange-bertalot). Volume 2. *Navicula* sensu stricto; 10 genera separated from *Navicula* sensu lato; *Frustulia*. A.R.G. Ganter Verlag K.G.

Lange-Bertalot, H.; Jahn, R. (2000). On the identity of *Navicula* (*Frustulia*) *rhomboides* and *Frustulia saxonica* (Bacillariophyceae). Systematic Geography of Plants 70: 255-261.

Lange-Bertalot, H.; Metzeltin, D. (1996). Indicators of Oligotrophy. 800 taxa representative of three ecologically distinct lake types. Iconographica Diatomologica 2: 1-390.

Lange-Bertalot, H.; Moser, G. (1994). *Brachysira*. Mongraphie der Gattung. Bibliotheca Diatomologica 29: 1-212.

Larned, S. T.; Scarsbrook, M.; Snelder, T.H.; Norton, N.J.; Biggs, B.J.F. (2004). Water quality in low-elevation streams and rivers of New Zealand: recent state and trends in contrasting land-cover classes. New Zealand Journal of Marine and Freshwater Research 38: 347–366.

Lawton, J. (1999). Are there general laws in ecology? Oikos 84(2): 177-192.

Leathwick, J.R.; Overton, J.M.; McLeod, M. (2003). An environmental domain analysis of New Zealand, and its application to biodiversity conservation. Conservation Biology 17: 1612–1623.

Lederer, L.; Soukupova, L., 2002: Biodiversity and ecology of algae in mountain bogs (Bohemian Forest, Central Europe). Archiv für Hydobiologie (Suppl) (Algol. Stud.) 106: 151-183.

Leibold, M., Holyoak, M.; Mouquet, N.; Amarasekare, P.; Chase, J.M.; Hoopes, M.F.; Holt, R.D.; Shurin, J.B.; Law, R.; Tilman, D.; Loreau, M.; Gonzales, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601-613.

Levine, J. (2000). Species diversity and biological invasions: relating local process to community pattern. Science 288: 852-854.

Levine, S.; D'Antonio, C. (1999). Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15-26.

Lim, D.S.S., Douglas, W.S.V.; Smol, J.P. (2001). Diatoms and their relationship to environmental variables from lakes and ponds on Bathurst Island, Nunavut, Canadian High Arctic. Hydrobiologia 450: 215 - 230.

Lindsay, W.L. (1867). On the Diatomaceae of Otago, New Zealand. Proceedings of the Linnean Society, Botany 9: 129-134.

Lindsay, W.L. (1867). On the Protophyta of New Zealand. Quarterly Journal of Microscopical Science. Volume VII. 97-113.

Lindsay, W.L. (1868). Contributions to New Zealand botany. Williams and Norgate, London and Edinburgh.

Lonsdale, W. (1999). Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522-1536.

Lotter, A.F.; Pienitz, R.; Schmidt, R. (1999). Diatoms as indicators of environmental change near arctic and alpine treeline. In Stoermer, E.F. & J. Smol (eds), The diatoms: applications for the environmental and earth sciences. Cambridge University Press: 205-226.

Lovei, G. (1997). Global change through invasion. Nature 388: 627.

Lowe, C.; Kemp, S.; Montagnes, D.J.S. (2005). An interdisciplinary approach to assess the functional diversity of free-living microscopic eukaryotes. Aquatic Microbial Ecology 41(67-77).

Lowe, D.J.; Green, J.D. (1987). Origins and development of the lakes. Pp. 1-64 in: Viner, A.B. (ed.). Inland Waters of New Zealand. DSIR, Wellington: 1-64.

Lowe, R.L. (1996). Periphyton patterns in lakes. Pp. 57-76 in:Stevenson, R.J.; Bothwell, M.L.; Lowe, R.L. (eds). Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, San Diego.

Lowe, R.L.; Morales, E.; Kilroy, C. (2006). *Frankophila biggsii* (Bacillariophyceae), a new diatom species from New Zealand. New Zealand Journal of Botany 44: 41-46.

Lundholm, N., Moestrup, O.; Kotaki, Y.; Horef-Emden, K.; Scholin, C.; Miller, P (2006). Inter- and intraspecific variation of the *Pseudo-nitzschia delicatissima* complex (Bacillariophyceae) illustrated by rDNA probes, morphological data and phylogenetic analyses. Journal of Phycology 42: 464-481.

MacDougall, A.; Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86: 42–55.

Magnuson, J.J.; Benson, B.J.; Kratz, T.K. (1990). Temporal coherence in the limnology of a suite of lakes in Winconsin, U.S.A. Freshwater Biology 23: 145-159.

Magurran, A. (2007). Species abundance distributions over time. Ecology Letters 10: 347-354.

Mäkilä, M.; Saarnisto, M.; Kankainen, T. (2001). Aapa mires as a carbon sink and source during the holocene. Journal of Ecology 89: 589 - 599.

Mann, D.G. (1988). Why didn't Lund see sex in *Asterionella*? A discussion of the diatom life cycle in nature. In: Round, F. E. (ed.). Algae and the Aquatic Environment. Bristol, Biopress Ltd. Pp. 384–412.

Mann, D.G. (1989). The diatom genus *Sellaphora*: separation from *Navicula*. British Phycological Journal 24: 1-20.

Mann, D.G. (1994). The origins of shape and form in diatoms: the interplay between morphogenetic studies and systematics. Pp. 24–26 in: Ingram, D. S.; Hudson, A. J. (eds). Shape and Form in Plants and Fungi. Academic Press, London.

Mann, D.G. (1999). The species concept in diatoms. Phycologia 38: 437–495.

Mann, D.G.; Droop, S. (1996). Biodiversity, biogeography and conservation of diatoms. Hydrobiologia 336: 19-32.

Mann, D.G.; McDonald, S.; Bayer, M.M.; Droop, S.J.M.; Chepurnov, V.A.; Loke, R.E.; Ciobanu, A.; du Buf, J.M.H. (2004). The *Sellaphora pupula* complex (Bacillariophyceae): morphometric analysis, ultrastructure and mating data provide evidence for five new species. Phycologia 43: 459-482.

Mark, A.F.; Johnson, P.N.; Dickinson, K.J.M.; McGlone, M.S. (1995). Southern hemisphere patterned mires, with emphasis on southern New Zealand. Journal of the Royal Society of New Zealand 25: 23-54.

Mataloni, G. (1999). Ecological studies on algal communities from Tierra del Fuego peat bogs. Hydrobiologia 391: 157-171.

Mataloni, G.; Tell, G. (1996). Comparative analysis of the phytoplankton communities of a peat bog from Tierra del Fuego (Argentina). Hydrobiologia 325: 101-112.

McCabe, S.; Cyr, H. (2006). Environmental variability influences the structure of benthic algal communities in an oligotrophic lake. Oikos 115: 197-206.

McCormick, P.; O'Dell, M. (1996). Quantifying periphyton responses to phosphorus in the Florida Everglades: a synoptic-experimental approach. Journal of the North American Benthological Society 15(4): 450-468.

McCormick, P.; Rawlik, P.; Lurding, K; Smith, EP; Sklar, FH (1996). Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. Journal of the North American Benthological Society 15: 433-449.

McGill, B. (2003a). Does Mother Nature really prefer rare species or are log-left-skewed SADs a sampling artefact? Ecology Letters 6: 766-773.

McGill, B.J. (2003b). A test of the unified neutral theory of biodiversity. Nature 422: 881-885.

McGlone, M.S. (2005). Goodbye Gondwana. Journal of Biogeography 32: 739-740.

McGlone, M.S.; Duncan, R. P.; Heenan, P. B. (2001). Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. Journal of Biogeography 28: 199-216.

McGlone, M.S.; Mark, A.F.; Bell, D. (1995). Late Pleistocene and Holocene vegetation history, Central Otago, South Island, New Zealand. Journal of the Royal Society of New Zealand 25: 1-22.

McLeod, D. (1974). Kingdom in the Hills: The Story of a Struggle. Whitcombe and Tombs, Christchurch.

McQueen, A.A.M.; Wilson, J.B. (2000). Vegetation and environment of a New Zealand raised bog. Journal of Vegetation Science 11: 547-554.

McQuoid, M. R.; Hobson, L.A. (1996). Review - Diatom resting stages. Journal of Phycology 32: 889 - 902.

Melbourne, B.; Cornell, H.; Davies, KF; Dugaw, CJ; Elmendorf, S; Freestone, AL; Hall, RJ; Harrison, S; Hastings, A; Holland, M; Holyoak, M; Lambrinos, J; Moore, K; Yokomizo, H (2007). Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters 10: 77-94.

Merton, P. (1987). The ecology of two South Westland pakihi mires. New Zealand Journal of Ecology 10: 165.

Metzeltin, D.; Lange-Bertalot, H. (1998). Tropical Diatoms of South America I. Iconographia Diatomologica 5. Koeltz Scientific Books.

Michelutti, N., Holtham, A.; Douglas, M.S.V.; Smol, J.P. (2003). Periphytic diatom assemblages from ultra-oligotrophic and UV transparent lakes and ponds on Victoria Island and comparisons with other diatom surveys in the Canadian Arctic. Journal of Phycology 39: 465-480.

Michelutti, N.; Douglas, M.S.V.; Lean, D.R.S.; Smol, J.P. (2002). Physical and chemical limnology of 34 ultra-oligotrophic lakes and ponds near Wynniatt Bay, Victoria Island, Arctic Canada. Hydrobiologia 482: 1-13.

Miller, R.; Death, R.G. (1997). Seasonal and spatial dynamics in the phytomacrofaunal community of Lake Henley, New Zealand. New Zealand Journal of Marine and Freshwater Research 31: 423-434.

Mitchell, A.; Meisterfeld, R. (2005). Taxonomic confusion blurs the debate on cosmopolitanism versus local endemism of free-living protists. Protist 156: 263-267.

Mizuno, M. (1991). Influence of cell volume on the growth and size reduction of marine and estuarine diatoms. Journal of Phycology 27: 473-478.

Moar, N.T. (1977). Post-glacial vegetation history of vegetation at Cass. Pp. 147-156 in Cass (ed. Burrows, C.J.). Dept. Botany, University of Canterbury.

Mölder, K.; Tynni, R. (1970). Über Finnlands rezente und subfossil Diatomeen IV. Bulletin of the Geological Society of Finland 42: 129–144.

Molot, L.A.; Dillon, P.J. (1997). Colour – mass balances and colour – dissolved organic carbon relationships in lakes and streams in central Ontario. Canadian Journal of Fisheries and Aquatic Sciences 54: 2789-2795.

Morales, E.; Siver, P.; Trainor, F. (2001). Identification of diatoms (Bacillariophyceaae) during ecological assessments: comparison between light microscopy and scanning electron microscopy techniques. Proceedings of the Academy of Natural Sciences of Philadelphia 151: 95–103.

Morgan, R. (2001). Soil formation processes. In Sturman, A. & R. Spronken-Smith (eds), The Physical Environment: a New Zealand perspective. Oxford University Press: 350-375.

Moser, G., Lange-Bertalot, H.; Metzeltin, D. (1998). Insel der Endemiten. Geobotanisches Phanomen Neukaledonien. Bibliotheca Diatomologica 38: 1-464. J. Cramer, Stuttgart.

Moser, G.; Steindorf, A.; Lange-Bertalot, H. (1995). Neukaledonien. Diatomeenflora einer Tropeninsel. Bibliotheca Diatomologica 32.

Moser, K.A.; MacDonald, G.M.; Smol, J.P. (1996). Applications of freshwater diatoms to geographical research. Progress in Physical Geography 20: 21 - 52.

Mosisch, T. (2001). Effects of desiccation on epilithic stream algae. New Zealand Journal of Marine and Freshwater Research 35: 173-179.

Mou, d.; Stoermer, E.F. 1992. Separating *Tabellaria* (Bacillariophyceae) shape groups based on Foureir descriptors. Journal of Phycology 28: 386-395.

Muñoz, J.; Aldosoro, J.; Negro, A.; de Hoyos, C.; Vega, J.C. (2003). Flora and water chemistry in a relictic mire complex: the Sierra Segundra mire area (Zamora, NW Spain). Hydrobiologia 495: 1-16.

Naeem, S.; Knops, J.M.H.; Tilman, D.; Howe, K.M.; Kennedy, T.; Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of co-varying extrinsic factors. Oikos 91: 97-108.

Negro, A.I.; De Hoyos, C.; Aldoroso, J.J. (2003). Diatom and desmid relationships with the environment in mountain lakes and mires of NW Spain. Hydrobiologia 505: 1-13.

Nichol, S. E.; Harvey, M.J.; Boyd, I.S. (1997). Ten years of rainfall chemistry in New Zealand. Clean Air 31: 30 - 37.

Norton, T.A.; Melkonian, M.; Andersen, R.A. (1996). Algal biodiversity. Phycologia 35: 308-320.

Orsini, L.; Procaccini, G.; Sarno, D.; Montresor, M (2004). Multiple rDNA ITS-types within the diatom *Pseudo-nitzschia delicatissima* (Bacillariophyceae) and their relative abundances across a spring bloom in the Gulf of Naples. Marine Ecology Progress Series 271: 87-98.

Owen, R.; Renaut, R.; Hover, V.C.; Ashley, G.M.; Muasya, A.M. (2004). Swamps, springs and diatoms: wetlands of the semi-arid Bogoria-Baringo Rift, Kenya. Hydrobiologia 518: 59-78.

Pace, M.L.; Cole, J.J. (2002). Synchronous variation of dissolved organic carbon and color in lakes. Limnology and Oceanography 47: 333-342.

Pantocsek, J. (1892). Beiträge zur Kenntnis der fossilen Bacillarien Ungarns. Teil 3. Süsswasser Bacillarien. Anhang: Analysen 15 neue Depots von Bulgarien, Japan, Mähren, Russlands und Ungarn, 42 Taf. Nagy-Tapolcsany.

Pantoscek, J. (1902). Die Bacillarien des Balatonsees. Resultate der Wissenschaftlichen Erforschung der Balatonees. Herausgegeben von der Balatonsee-Commission der Ugn. Wein, Geographischen Gesellschaft. 112 p.

Pantoscek, J. (1905). Beschreibung neuer Bacillarien, welche in der Pars III der “Beiträge zur Kenntnis der fossilen Bacillarien Ungarns”, abgebildet wurden. Pozsony. 118 p.

Parker, I.; Simberloff, D.; Lonsdale, W.M.; Goodell, K.; Wonham, M.; Kareiva, P.M.; Williamson, M.H.; Von Holle, B.; Moyle, P.B.; Byers, J.E.; Goldwasser, L. (1999). Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3-19.

Parmesan, C., Gaines, S.; Gonzales, L.; Kaufman, DM.; Kongsolver, J.; Townsend-Petersen, A.; Sagarin, R (2005). Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108: 58-75.

Passy, S. I. (2001). Spatial paradigms of lotic diatom distribution: a landscape ecology perspective. Journal of Phycology 37: 370-378.

Pastor, J.; Solin, J.; Bridgham, S.D.; Updegraff, K.; Harth, C.; Weishampel, P.; Dewey, B. (2003). Global warming and the export of dissolved organic carbon from boreal peatlands. Oikos 100: 380-386.

Patrick, R.; Reimer, C.W. (1966, 1975). The diatoms of the United States. Monographs of the Academy of Natural Sciences of Philadelphia, Volume 1. Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae, p. 1-688; volume 2: Entomoneidae, Cymbellaceae, Gomphonemaceae, Epithemiaceae, p. 1-213.

Petersen, C. (1996). Response of benthic algal communities to natural physical disturbance. Pp. 375-402 in: Stevenson, R.J.; Bothwell, M.L.; Lowe, R.L. (eds). Algal Ecology: Freshwater benthic ecosystems. Academic Press, San Diego.

Peterson, C., Hoagland, K. (1990). Effects of wind-induced turbulence and algal mat development on epilithic diatom succession in a large reservoir. Archiv für Hydrobiologie 118: 47-68.

Pienitz, R.; Smol, J.P. (1993). Diatom assemblages and their relationship to environmental variables in lakes from the boreal forest - tundra ecotone near Yellowknife, Northwest Territories, Canada. Hydrobiologia 269/270: 391-404.

Pollock, M.; Naiman, R.; Hanley, T.A. (1998). Plant species richness in riparian wetlands – a test of biodiversity theory. Ecology 79: 94–105.

Proctor, M.C.F. (1994). Seasonal and shorter-term changes in surface-water chemistry on four English ombrogenous bogs. Journal of Ecology 82: 597-610.

Proctor, M.C.F. (2006). Temporal variation in the surface-water chemistry of a blanket bog on Dartmoor, southwest England: analysis of 5 years' data. European Journal of Soil Science 57: 167-178.

Proctor, M.C.F.; Maltby, E. (1998). Relations between acid atmospheric deposition and the surface pH of some ombrotrophic bogs in Britain. Journal of Ecology 86: 329-340.

Psenner, R. (1989). Chemistry of high mountain lakes in siliceous catchments of the Central Eastern Alps. Aquatic Science 51: 108-128.

Racca, J.; Prairie, Y. (2004). Apparent and real bias in numerical transfer functions in palaeolimnology. Journal of Paleolimnology 31: 117-124.

Rasmussen, J.B.; Godbout, L.; Schallenburg, M. (1989). The humic content of lake water and its relationship to watershed and lake morphometry. Limnology and Oceanography 34: 1336-1343.

Reche, I.; Pace, M.L.; Cole, J.J. (1999). Relationship of trophic and chemical conditions to photobleaching of dissolved organic matter in lake ecosystems. Biogeochemistry 44: 259-280.

Reid, M. (2005). Diatom-based models for reconstructing past water quality and productivity in New Zealand lakes. Journal of Paleolimnology 33: 13-38.

Reid, M.R.; Kim, J.P.; Hunter, K.A. (1999). Trace metal and major ion concentrations in Lakes Hays and Manapouri. Journal of the Royal Society of New Zealand 29: 245-255.

Rejmanek, M.; Richardson, D. (1996). What attributes make some plants more invasive? Ecology 77: 1655-1661.

Renberg, I. (1977). *Fragilaria lata*, a new diatom species. Botanisker Notiser 130: 315–318

Reynolds, C.S. (1993). Scales of disturbance and their role in plankton ecology. Hydrobiologia, 249: 157-171.

Rosenweig, M. (2001). The four questions: what does the introduction of exotic species do to diversity? Evolutionary Ecology Research 3: 361-367.

Ross, R., Cox, E.J.; Karayeva, N.I.; Mann, D.G.; Paddock, T.B.B.; Simonsen, R.; Sims, P.A. (1979). An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia Beiheft 64: 513-533.

Round, F.E. (1972). The problem of reduction of cell size during diatom cell division. Nova Hedwigia 23: 291–303.

Round, F.E. (1996). Opinion. What characters define diatom genera, species and infraspecific taxa? Diatom Research 11: 203–218.

Round, F.E.; Bukhtiyarova, L. (1996). Four new genera based on *Achnanthes* (*Achnanthidium*) together with a re-definition of *Achnanthidium*. Diatom Research 11: 345 - 361.

Round, F.E.; Crawford, R.M.; Mann, D.G. (1990). The Diatoms. Biology and morphology of the genera. Cambridge University Press, Cambridge.

Round, F.E.; Mann, D.G. (1981). The diatom genus *Brachysira*. I. Typification and separation from *Anomoeoneis*, Archiv für Protistenkunde 124: 221-231.

Round, F.E.; Williams, D.M. (1992): The generic status of some diatom genera with special reference to the araphid group – a reply. Nova Hedwigia 55: 485–500.

Rumrich, U.; Lange-Bertalot, H.; Rumrich, M. (2000). Diatomeen der Anden (diatoms of the Andes from Venezuela to Patagonia / Tierra del Fuego. A.R.G. Ganter Verlag K.G

Sabbe, K.; Hodgson, D.; Verleyen, E.; Taton, A.; Wilmotte, A.; Vanhoutte, K.; Vyverman, W. (2004). Salinity, depth and the structure and composition of microbial mats in continental Antarctic lakes. Freshwater Biology 49: 296-319.

Sabbe, K.; Vanhoutte, K.; Lowe, R.L.; Bergey, E.A.; Biggs, B.J.F.; Francouer, S.; Vyverman, W. (2001). Six new *Actinella* (Bacillariophyta) species from Papua New Guinea, Australia and New Zealand: further evidence for widespread diatom endemism in the Australasian region. European Journal of Phycology 36: 321-340.

Sabbe, K.; Vanhoutte, K.; Vyverman, W. (2000). *Actinella comperei* sp. nov. (Eunotiaceae, Bacillariophyta): a new endemic diatom from Tasmania (Australia). Systematics and Geography of Plants 70: 237–243.

Sakai, S.; Allendorf, F.; Holt, J.S.; Lodge, D.M.; Molofsky, J.; With, K.A.; Baughman, S.; Cabin, R.J.; Cohen, J.E.; Ellstrand, N.C.; McCauley, D.E.; O'Neil, P.; Parker, I.M.; Thompson, J.N.; Weller, S.G. (2001). The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305-332.

Sarno, D.; Kooistra, W.; Medlin, L. K.; Percopo, I.; Zingone, A (2005). Diversity in the genus *Skeletonema* (Bacillariophyceae). II. An assessment of the taxonomy of *S. costatum*-like species with the description of four new species. Journal of Phycology 41: 151-176.

Sax, D.; Brown, J. (2000). The paradox of invasion. Global Ecology and Biogeography 9: 363-371.

Sax, D.; Gaines, S.; Brown, J.H. (2002). Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. The American Naturalist 160: 766-783.

Scharf, F.; Juanes, F.; Sutherland, M. (1998). Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. Ecology 79: 448–460.

Scherer, R. (1988). Freshwater diatom assemblages and ecology/palaeoecology of the Okefenokee swamp/marsh complex, Southern Georgia, U.S.A. Diatom Research 3: 129-157.

Schmidt, A. (1913). Tafel 297 in Atlas der Diatomaceen-Kunde. Leipzig, R. Reisland. (Index: Hanna, G.D. 1969: Bibliotheca Diatomologica 10: 1–208.)

Schmidt, A., Schmidt, M.; Fricke, F.; Heiden, H.; Müller, O.; Hustedt, F. (1874 – 1959). Atlas der Diatomaceen-Kunde. Index by Hanna, G.D. (1969). Bibliotheca Phycologica Band 10. J. Cramer.

Sharma, N.; Rai, A.; Singh, S.; Brown, R.M.Jr (2007). Airborne algae: their present status and relevance. Journal of Phycology 43: 615-627.

Shayler, H.A.; Siver, P.A. (2004). Description of a new species of the diatom genus *Brachysira* (Bacillariophyta), *Brachysira gravida* sp. nov. from the Ocala National Forest, Florida, U.S.A. Nova Hedwigia, 78: 399-409.

Sheridan, R. P. (2001). Role of ultraviolet radiation in maintaining the three-dimensional structure of a cyanobacterial mat community and facilitating nitrogen fixation. Journal of Phycology 37: 731 - 737.

Siegel, D.I.; Glaser, P.H.; So, J.; Janecky, D.R. (2005). The dynamic balance between organic acids and circumneutral groundwater in a large boreal peat basin. Journal of Hydrology 320: 421-431.

Simonsen, R. (1987). Atlas and catalogue of the diatom types of Friedrich Hustedt. Berlin, J. Cramer, Stuttgart. 772 p.

Sims, P.A.; Mann, D.G.; Medlin, L.K. (2006). Evolution of the diatoms: insights from fossil, biological and molecular data. Phycologia 45: 361-402.

Siver, P.A.; Baskette, G. (2004). A morphological examination of *Frustulia* (Bacillariophyceae) from the Ocala National Forest, Florida, USA. Canadian Journal of Botany 82: 629-644.

Siver, P.A.; Hamilton, P.B. (2005). Observations on new and rare species of freshwater diatoms from Cape Cod, Massachusetts, USA. Canadian Journal of Botany 83: 362-378.

Sjörs, H.; Gunnarsson, U. (2002). Calcium and pH in north and central Swedish mire waters. Journal of Ecology 90: 650-657.

Skuja, H. (1976). Zur Kenntis der Algen Neuseelandisher Torfmoore. Nova Actae Regiae Societatis Scientarum Upsaliensis. Ser. V. C. Vol. 2.

Smith, D.G.; Maasdam, R. (1994). New Zealand National River Water Quality Network. 1. Design and physico-chemical characterization. New Zealand Journal of Marine and Freshwater Research 28: 19-35.

Smith, V.H.; Foster, B.L.; Grover, J.P.; Holt, R.D.; Leibold, M.A.; Denoyelles, F. (2005). Phytoplankton species richness scales consistently form laboratory microcosms to the world's oceans. Proceedings of the National Academy of Sciences of the United States of America 102: 4393-4396.

Smol, J. P.; Cumming, B.F. (2000). Tracking long-term changes in climate using algal indicators in lake sediments. Journal of Phycology 36: 986 - 1011.

Snelder, T.; Biggs, B.J.F. (2002). Multiscale river environment classification for water resources management. Journal of the American Water Resources Association 38: 1225–1239.

Snyder, R. (2007). Spatiotemporal population distributions and their implications for species coexistence in a variable environment. Theoretical Population Biology 72: 7-20.

Snyder, R.; Chesson, P. (2003). Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. Ecology Letters 6: 301-309.

Soininen, J. (2006). Local and regional coexistence of diatoms - on the mechanisms promoting high local diatom species richness. Diatom Research 21: 217-223.

Soininen, J.; Heino, J. (2005). Relationships between local population persistence, local abundance and regional occupancy of species: distribution patterns of diatoms in boreal streams. Journal of Biogeography 32: 1971-1978.

Somerfield, P.J.; Clarke, K.R.; Olsgard, F. (2002). A comparison of the power of categorical and correlational tests applied to community ecology data from gradient studies. Journal of Animal Ecology 71: 581–593.

Sommaruga-Wograth, S.; Koinig, K.A.; Schmidt, R.; Sommaruga, R.; Tessadri, R.; Psenner, R. (1997). Temperature effects on the acidity of remote alpine lakes. Nature 387:64-76.

Souza, M.G.M.; Compère, P. (1999). New diatom species from the Federal District of Brazil. Diatom Research 14: 357-366.

Sparling, J. (1966). Studies on the relationship between water movement and water chemistry in mires. Canadian Journal of Botany 44: 747-758.

Stevenson, R.J. (1996). An introduction to algal ecology in freshwater benthic habitats. Chapter 1 in Stevenson, R.J.; Bothwell, M.L.; Lowe, R.L. (eds). Algal Ecology: Freshwater benthic ecosystems. Academic Press, San Diego.

Stevenson, R.J.; Pan, Y. (1999). Assessing environmental conditions in rivers and streams with diatoms. Pp. 11-40 in Stoermer, E.F.; Smol, J.(eds), The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, New York.

Stoermer, E. F.; Ladewski, T.; Kociolek, J. (1986). Further observations on *Gomphoneis*. Pp. 205-213 in Ricard, M. (ed.) Eighth International Diatom Symposium, Paris. Koeltz, Koenigstein.

Stohlgren, T.J.; Binkley, D.; Chong, G.W.; Kalkhan, M.A.; Schell, L.D.; Bull, K.A.; Otsuki, Y.; Newman, G.; Bashkin, M.; Son, Y. (1999). Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25-46.

Tahvanainen, T.; Sallantus, T.; Heikkilä, R. (2003). Seasonal variation of water chemistry gradients in three boreal fens. Annales Botanica Fennici 40: 345-355.

Tahvanainen, T.; Sallantus, T.; Heikkilä, R.; Tolonen, K. (2002). Spatial variation of mire surface water chemistry and vegetation in northeastern Finland. Annales Botanica Fennici 39: 235-251.

Theriot, E. (1992). Clusters, species concepts and morphological evolution of diatoms. Systematic Biology 41: 141-157.

Thomson, D. (2005). Measuring the effects of invasive species on the demography of a rare endemic plant. Biological Invasions 7: 615-624.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion and community assembly. Proceedings of the Academy of Natural Sciences of the United States of America 101: 10854-10861.

Timperley, M.; Vigor-Brown, R.; Kawashima, M.; Ishigami, M. (1985). Organic nitrogen compounds in atmospheric precipitation: their chemistry and availability to phytoplankton. Canadian Journal of Fisheries and Aquatic Sciences 42: 1171-1177.

Trewick, S.A.; Paterson, A.M.; Campbell, H.J. (2007). Hello New Zealand. Journal of Biogeography 34: 1 – 6.

Tyler, P. A. (1996). Endemism in freshwater algae. Hydrobiologia 336: 127 - 135.

Van der Vijver, B. (2002). *Frustulia cirisae* sp. nov., a new aerophilous diatom from Ile de la Possesion (Crozet Archipelago, Subantarctica). Diatom Research 17: 415 – 421.

Van der Vijver, B.; Frenot, Y.; Beyens, L. (2002). Freshwater diatoms from Ile de la Possesión (Crozet Archipelago, Subantarctica). Bibliotheca Diatomologica 46. J. Cramer

Vanhoutte, K.; Verleyen, E.; Kilroy, C.; Sabbe, K.; Dasseville, R.; Vyverman, W. (2006a). Catchment characteristics and chemical limnology of small lakes, tarns and mire pools in New Zealand (South Island) and Tasmania. Marine and Freshwater Research 57: 83-93.

Vanhoutte, K.; Verleyen, E.; Sabbe, K.; Kilroy, C.; Sterken, M.; Vyverman, W. (2006b). Congruence and disparity in benthic diatom community structure of small lakes in New Zealand and Tasmania. Marine and Freshwater Research 57: 789-801.

Vanhoutte, K.; Verleyen, E.; Vyverman, W.; Chepurnov, V.; Sabbe, K. (2004). The freshwater diatom genus *Kobayasiella* (Bacillariophyta) in Tasmania, Australia. Australian Systematic Botany 17: 483-496.

VanLandingham, S.L. (1967 – 1979). Catalogue of the fossil and recent genera and species of diatoms and their synonyms. Vols. I – VIII. J. Cramer, Vaduz.

Vanormelingen, P.; Chepurnov, V.A.; Mann, D.G.; Cousin, S.; Sabbe, K.; Vyverman, W. 2007. Congruence of morphological, reproductive and ITS rDNA sequence data in some Australasian *Eunotia bilunaris* (Bacillariophyta). European Journal of Phycology 42: 61-79.

Verhoeven, W.; Herrmann, R.; Eiden, R.; Klemm, O. (1987). A comparison of the chemical composition of fog and rainwater collected in the Fichtelgebirge, Federal Republic of Germany, and from the South Island of New Zealand. Theoretical and Applied Climatology 38: 210 - 221.

Verleyen, E.; Hodgson, D.A.; Vyverman, W.; Roberts, D.; McMinn, A.; Vanhoutte, K.; Sabbe, K. (2003). Modelling diatom response to climate induced fluctuations in the moisture balance in continental Antarctic lakes. Journal of Paleolimnology 30: 195-215.

Vilenkin, B. and V. Chikatunov (2000). Participation of species with different zoogeographical ranks in the formation of local faunas: a case study. Journal of Biogeography 27: 1201-1208.

Villeneuve, V.; Vincent, W.; Komárek, J. (2001). Community structure and microhabitat characteristics of cyanobacterial mats in an extreme high Arctic environment: Ward Hunt Lake. Nova Hedwigia Beiheft 123: 199-224.

Vincent, W.; Downes, M.; Castenholz, R.W.; Howard-Williams, C. (1993). Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. European Journal of Phycology 28: 213-221.

Vincent, W.; Pienitz, R. (1996). Sensitivity of high-latitude freshwater ecosystems to global change: temperature and ultraviolet radiation. Geoscience Canada 23: 231-236.

Vitousek, P.; D'Antonio, C.; Loope, L.L.; Rejmanek, M.; Westbrooks, R (1997). Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1-16.

Vitt, D.H.; Bayley, S.E.; Jin, T.-L. (1995). Seasonal variation in water chemistry over a bog-rich fen gradient in Continental Western Canada. Canadian Journal of Fisheries and Aquatic Sciences 52: 587 - 606.

Vyverman, W. (1991). Diatoms from Papua New Guinea. Bibliotheca Diatomologica 22: 1–224.

Vyverman, W., Sabbe, K.; Mann, D.G.; Kilroy, C.; Vyverman, R.; Vanhoutte, K.; Hodgson, D. (1998). *Eunophora* gen. nov. (Bacillariophyta) from Tasmania and New Zealand: description and comparison with *Eunotia* and amphoroid diatoms. European Journal of Phycology 33: 95-111.

Vyverman, W.; Sabbe, K.; Vyverman, R. (1997). Five new species of *Biremis* (Bacillariophyta) from Tasmania. Phycologia 36: 91-102.

Vyverman, W.; Verleyen, E.; Sabbe, K. (and 13 others) (2007b). Historical processes constrain patterns in global diatom diversity. Ecology 88: 1924-1931.

Vyverman, W.; Vyverman, R.; Hodgson, D.; Tyler, P (1995). Diatoms from Tasmanian mountain lakes: a reference data-set (TASDIAT) for environmental reconstruction and a systematic autecological study. Bibliotheca Diatomologica 33: 1-193.

Vyverman, W.; Vyverman, R.; Rajendran, V.S.; Tyler, P. (1996). Distribution of benthic diatom assemblages in Tasmanian highland lakes and their possible use as indicators of environmental changes. Canadian Journal of Fisheries and Aquatic Sciences 53: 493 - 508.

Vyverman, W; Verleyen, E; Sabbe, K. (2007a). Biogeography of freshwater microalgae. In: McCarthy PM & Orchard AE (eds), Algae of Australia: Introduction. ABRS, Canberra; CSIRO Publishing, Melbourne. p. 580-593.

Walker, S.; Steel, J.B.; Rapson, G.L.; Rosxburgh, S.H.; King, W.M.; Watkins, A.J.; Myers, T.E.; Keogh, J.A.; McQueen, A.A.M.; Bastow Wilson, J. (2001). A *Chionocloa* /*Sphagnum* / cushion valley bog in east Otago, New Zealand. New Zealand Journal of Ecology 25: 39-52.

Wardle, P. (1981). Bog pine areas on Oxnams Plain, Tutaki Valley, Nelson. Unpublished Botany Division vegetation report. DSIR, Botany Division, Lincoln.

Watanabe, M.W.; Mayama, S.; Hiroki, M.; Nozaki, H. 2000. Biomass, species composition and diversity of epipelic algae in mire pools. Hydrobiologia 421: 91-102.

Wetzel, R.G., 2001. Limnology. Lake and River Ecosystems. Academic Press, San Diego.

Wheeler, B.; Proctor, M. (2000). Ecological gradients, subdivisions and terminology of north-west European mires. Journal of Ecology 88: 187-203.

Wiggli, M.; Smallcombe, A.; Bachofen, R. (1999). Reflectance spectroscopy and laser confocal microscopy as tools in an ecophysiological study of microbial mats in an alpine bog pond. Journal of Microbiological Methods 34: 173-182.

Wilkinson, D. (2001). What is the upper size limit for cosmopolitan distribution in free-living microorganisms? Journal of Biogeography 28: 285-291.

Wilkinson, K.J.; Jones, H.G.; Campbell, R.G.C.; Lachance, M. (1992). Estimating organic acid

contributions to surface water acidity in Quebec (Canada). Water, Air, and Soil Pollution 61: 57-74.

Williams, D.M. (1990). *Fragilaria floridana* Hanna: ultrastructure of the valve and girdle and its transference to *Fragilariforma* Williams & Round. Pp. 259–265 in: Ricard, M. (ed.). Ouvrage dedie à la memoire du Professor Henri Germain (1903–1989). Koeltz Scientific Books..

Williams, D.M. (1996a). Notes on the genus *Fragilariforma* (Fragilariophyceae: Bacillariophyta) with a description of a new Miocene species, *Fragilariforma platensis*. Nova Hedwigia Beiheft 112: 283–288.

Williams, D.M. (1996b). Fossil species of the diatom genus *Tetracyclus* (Bacillariophyta, '*ellipticus*' species group): morphology, interrelationships and the relevance of ontogeny. Philosophical Transactions of the Royal Society, London, Series B 351: 1759-1782.

Williams, D.M.; Round, F.E. (1987). Revision of the genus *Fragilaria*. Diatom Research 2: 267–288.

Williams, D.M.; Round, F.E. (1988). *Fragilariforma*, nom. nov., a new generic name for *Neofragilaria* Williams & Round. Diatom Research 3: 265–267.

Willig, M.R.; Kaufman, D.M.; Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual review of Ecology, Evolution and Systematics 34: 273-309.

Winter, J.; Duthie, H. (2000). Epilithic diatoms as indicators of stream total N and total P concentration. Journal of the North American Benthological Society 19: 32-49.

Wolfe, W.P.; Kling, H.J. (2001). A consideration of some North American soft-water *Brachysira* taxa and description of *B. arctoborealis* sp. nov. Pp. 243-269 in: Jahn, R.; Kociolek, J.P.; Witkowski, A.; Compère, P. (eds). Studies on Diatoms: Lange-Bertalot Festschrift,. Ganter Verlag KG.

Worrall, F.; Burt, T.P.; Jaeban, R.Y.; Warburton, J.; Shedden, R. (2002). Release of dissolved organic carbon from upland peat. Hydrological Processes 16: 3487-3504.

Wright, S. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130: 1-14.

Wu, F.C.; Mills, R.B.; Cai, Y.R.; Evans, R.D.; Dillon, P.J. (2005). Photodegradation-induced changes in dissolved organic matter in acidic waters. Canadian Journal of Fisheries and Aquatic Sciences 62: 1019-1027.

Yacobi, Y.Z.; Alberts, J.J.; Takacs, M.; McElvaine, M. (2003). Absorption spectroscopy of colored dissolved organic carbon in Georgia (USA) rivers: the impact of molecular size distribution. Journal of Limnology 62: 41-46.

Yurkonis, K.; Meiners, S. (2004). Invasion impacts local species turnover in a successional system. Ecology Letters 7: 764-769.

Zobel, M. (1997). The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology and Evolution 12: 266-269.